Neural Correlates of Sentence-Level Rhyme Processing

Thesis (cumulative thesis)

Presented to the Faculty of Arts and Social Sciences

of the University of Zurich

for the Degree of Doctor of Philosophy

by

Martina Andrea Hurschler

Accepted in the Spring Term 2014

on the Recommendation of the Doctoral Committee:

Prof. Dr. Martin Meyer (main advisor)

Prof. Dr. Volker Dellwo

Zurich, 2015

ACKNOWLEDGEMENTS

First of all, I would like to thank my supervisor, Prof. Dr. Martin Meyer for his tremendous support, his scientific guidance, and his motivation in difficult phases of this project.

Then I would also like to thank Prof. Dr. Lutz Jäncke for giving me the opportunity to work in his department and all the co-workers in the department for a cheerful and friendly atmosphere and fruitful scientific discussions. Special thanks go to Franziskus Liem, Mathias Oechslin, and Philipp Stämpfli for their cooperation on my projects and to Katharina Rufener, Ladina Bezzola, and Luana Amato for their support during fMRI measurements.

Many thanks also to Volker Dellwo for being part of the committee.

Further I would like to thank all the volunteers for their participation in the experiments – this work would not have been possible without them.

Most of all, I express my deepest gratitude to my parents Margrit and Otto and my siblings Fabienne, Patrick and Marion for all their love and encouragement. Finally, my warmest thank goes to Thomas for giving me so much emotional support during stressful times and to our little ones, Amélie and Leonel, for filling my life with joy.

ABSTRACT

Rhyme detection is commonly considered to form one of the earliest developing parts of phonological awareness and the ability to rhyme has been linked to the development of different language functions such as learning to read. Despite these evidenced practical implications, to date, there exists hardly any knowledge concerning the neural underpinnings of auditory rhyme processing at sentence-level.

Furthermore, the topic is of specific interest regarding the question of functional lateralization in speech processing. Despite the well-documented predominance of the left hemisphere for most domains within speech processing, increasing evidence from neuroimaging studies proposes an essential involvement of the right hemisphere to the processing of speech perception. This dissertation focuses on functional lateralization during auditory language processing and in particular on the contribution of the right hemisphere to specific processes of speech perception.

Through two functional magnetic resonance imaging studies, this thesis aims to investigate brain processes associated with auditory rhyme processing at sentence level and to provide first insights into the influence of metrics on neural correlates of rhyme processing.

The first study employed a simple rhyme detection task with metrical pseudo-sentences. Results show right-lateralized activation in perisylvian regions and left-lateralized activation of the anterior insula as well as the opercular part of the inferior frontal gyrus during rhymed as compared to non-rhymed stimuli.

Additionally in the second study, metrics of the pseudo-sentences were varied in order to investigate influences of metrics on rhyme processing. Results not only replicated findings of the first study but in addition showed a positive interaction effect of rhyme and meter in the right superior temporal sulcus and the right putamen.

Taken together, this thesis provides novel insight into neural correlates of sentence-level rhyme detection and its modulation by metrics in healthy adults.

ZUSAMMENFASSUNG

Die Fähigkeit, Reime zu erkennen, zählt zu einer der am frühesten entwickelten Fertigkeiten im Rahmen des Konzepts der phonologischen Bewusstheit und wurde in diversen Studien mit der Entwicklung verschiedener Sprachfunktionen – wie beispielsweise der Lesekompetenz – in Verbindung gebracht. Trotz der gut belegten praktischen Relevanz des Themas existieren bisher kaum gesicherte Erkenntnisse über die neuronalen Grundlagen von auditorischer Reimverarbeitung auf Satzebene.

Das Thema ist zudem von spezifischem Interesse bezüglich der Frage der funktionalen Lateralisierung während der Verarbeitung von gesprochener Sprache. Obwohl die Dominanz der linken Hemisphäre in den meisten Domänen der Sprachverarbeitung gut belegt ist, häuft sich die Evidenz aus bildgebenden Studien für eine massgebliche Beteiligung der rechten Hemisphäre in unterschiedlichen Prozessen der Sprachwahrnehmung. Der Fokus dieser Arbeit liegt auf der funktionellen Lateralisierung der beiden Hemisphären und insbesondere dem Beitrag der rechten Hemisphäre während spezifischer Prozesse der auditorischen Sprachwahrnehmung.

Diese Dissertation untersucht mittels zweier funktioneller magnetresonanztomographischer Studien die neuronalen Grundlagen von Reimverarbeitung auf Satzebene sowie den Einfluss von Metrik auf diese Prozesse.

Die Resultate der ersten Studie zeigen einerseits rechts-lateralisierte Aktivierung in perisylvischen Regionen während einer einfachen Reimaufgabe und andererseits links-lateralisierte Aktivität der anterioren Insula und des pars opercularis des inferioren frontalen Gyrus bei der Verarbeitung gereimter Sätze.

In der zweiten Studie wurde eine komplexere Aufgabe verwendet und die Metrik der Pseudosätze variiert. Die Resultate replizieren nicht nur Ergebnisse der ersten Studie, sondern weisen auch auf einen wesentlichen Einfluss von Metrik auf die neuronalen Prozesse bei der auditorischen Reimverarbeitung hin.

Abschliessend werden diese Ergebnisse im Rahmen vorgeschlagener neurokognitiver Modelle diskutiert und weitere Fragestellungen und Forschungsthemen vorgestellt.

CONTENTS

1. INTRODUCTION

Rhymes are not only one of the most characteristic features of poetry, but also play a role in everyday language. Different types of rhymes are employed in infant-directed speech and nursery rhymes and rhyming mnemonics are a frequently used tool to learn things - such as the alphabet or tone order. To date, the neural basis of rhyme processing at sentence-level is largely unknown. The present thesis aims to fill this gap by investigating the brain areas involved in rhyme detection by means of two consecutive functional magnetic resonance imaging (fMRI) studies.

In a general sense this thesis thereby aims to further investigate the division of labor between the two hemispheres during language processing and in particular to contribute to the topic of right hemispheric contribution to speech processing. In recent years, an increasing number of neuroimaging studies have been concerned with the investigation of processing suprasegmental auditory and speech cues, such as prosody and speech rhythm (e.g. Booth et al., 2004; Geiser, Zaehle, Jancke, & Meyer, 2008; Meyer, Alter, Friederici, Lohmann, & von Cramon, 2002; Meyer, Steinhauer, Alter, Friederici, & von Cramon, 2004) and an essential involvement of the right (usually non-dominant) hemisphere in such processes has become more and more apparent. Different models have been proposed to account for lateralization during speech processing. Increasing attention has recently been paid to approaches to understand lateralization processes during speech processing in auditory-related cortices on the basis of different temporal integration processes (e.g. Poeppel, 2003; Zatorre & Belin, 2001), thus stating the two hemispheres to be specialized for processing speech cues in different temporal resolutions. This thesis proposes that experimental paradigms employing rhyme detection tasks with pseudo-sentences are suitable to evoke lateralized brain responses and specific right hemispheric cortical activations that can be explained on the basis of "asymmetric sampling in time" during speech perception (Poeppel, 2003). This notion has been investigated in two empirical studies (see Chapter 4).

In order to embed the studies into a broader theoretical context, the first part of Chapter 2 will briefly outline the history of cognitive neuroscience of language and speech processing, and present some influential models of language processing. The focus will then turn to predictions about lateralization in speech perception based on the temporal nature of speech, and processes involved in rhyme processing will briefly be outlined.

Chapter 3 summarizes the relevance of the research topic and states the research questions addressed by the empirical studies. The original research articles of these two studies are presented in Chapter 4, followed by a general discussion (Chapter 5) that relates the findings of the studies to the stated questions, puts them into a broader research context and identifies limitations and implications for future work in the field.

2. THEORETICAL BACKGROUND

2.1 Functional anatomy of language and speech processing

2.1.1 The classical model of language processing

Until about 30 years ago, knowledge of the cerebral basis of language processing was mainly based on a lesion-deficit model and thus understanding of the neural correlations of language and speech processing relied on studies regarding impairments in patients with brain damage or patients undergoing electrical stimulation in the context of neurosurgery (Price, 2012).

The classical model of language processing in the brain originated about 150 years ago with the work of Broca, Wernicke, and Lichtheim, and has been extremely influential in discussions of the neural basis of language. The main predictions of this model have guided clinical practice for decades.

In 1861, the French neurologist Paul Broca reported a case-study of a patient most strongly impaired in articulating language. Post-mortem inspection of the patient's brain revealed damage encompassing the third frontal convolution in the left hemisphere. As a consequence, he suggested the damaged area – later referred to as 'Broca's area' – to contain the motor images of speech and thus to be essentially involved in language production (Broca, 1861).

Similarly, in the 1870s, the German physician Carl Wernicke described two cases of patients with enormous difficulties in understanding spoken language after an insult in the left hemisphere. The post-mortem autopsy of one of the patients showed damage in posterior regions of the left superior temporal sulcus. This region – subsequently referred to as 'Wernicke's area' – was associated with auditory images of speech. Based on Meynert's (Meynert, 1866) concepts of association fibers, Wernicke constructed a model of neuropsychological deficits evolving not only as a consequence of damage to a particular brain region, but also possibly resulting from lesions to ascending and descending pathways. In support of his arguments he referred to cases of connection aphasia, resulting from lesions to the fasciculus arcuatus, which links auditory with motor regions (Wernicke, 1874).

In 1885, Lichtheim presented an elaboration of this model consisting of three main centers for auditory or oral language processing: While language perception was assumed to involve

'Wernicke's area' and language production 'Broca's area', he additionally proposed diffuse connecting regions to be responsible for semantic processing, thus generating the famous "house" scheme (see Figure 1). Although Lichtheim's model was not able to account for the complexity of the processes involved in language production and comprehension, it served as an important framework for the conceptualization of the language-processing network.

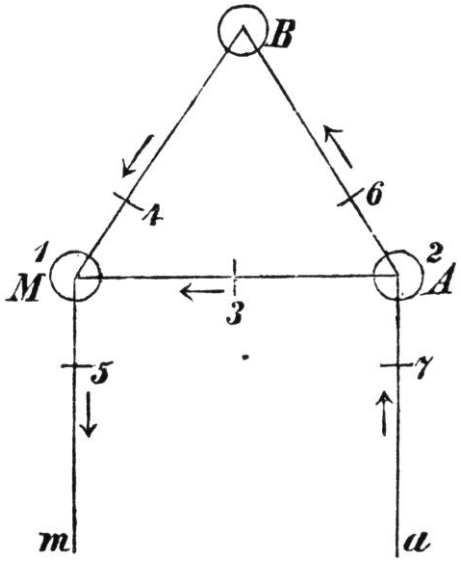

Figure 1. Lichtheim's model (house diagram). A: word representation center, B: conceptual center, M: motor center (Figure from Eling, 2011).

The Broca-Wernicke-Lichtheim model stands for an early attempt to characterize complex behavior in neuroanatomical terms and thus laid the foundation for the principle of functional neuroanatomical localization (Ben Shalom & Poeppel, 2008).

Finally it was Norman Geschwind (Geschwind, 1965) who brought the classical model back into scientific discourse by further elaborating it and suggesting a localized substrate for semantic processing involving the inferior parietal cortex.

2.1.2 Insights from functional neuroimaging studies

With the development of increasingly articulated linguistic and psycholinguistic models on one side, and the advent of neuroimaging methods on the other side, it became evident that the classical neurological model of language processing is anatomically as well as linguistically underspecified (Poeppel & Hickok, 2004; Ben Shalom & Poeppel, 2008). The

development of positron emission tomography (PET), followed by the introduction of functional magnetic resonance imaging (fMRI), made high-resolution brain imaging widely available and brought about a lot of progress in the understanding of neuroscience of language. The central assumptions of the classical model were extensively reevaluated.

In particular, the classical model's notion of two distinct left hemispheric speech centers, responsible for all essential expressive and perceptive language functions, proved not to be tenable anymore. Early neuroimaging studies not only showed regions outside the classical language centers to be involved in language processing (Binder et al., 1997; Binder, Frost, Hammeke, Rao, & Cox, 1996), but the notion of homogenously organized areas implicated by the classical model was also refuted by studies using new techniques (Amunts & Zilles, 2012; Wise et al., 2001). Cytoarchitectural studies showed that the canonical "Broca's area" is composed of a number of cytoarchitectonically different areas, thus making it unlikely that this region can be treated as one unified area (Amunts et al., 2010; Amunts & Zilles, 2012). Moreover, functional imaging studies reported involvement of this region in a far greater number of different functions than originally assumed.

The classical model's claim of language specificity of the two primary language areas is therefore also not compatible with findings from neuroimaging studies. Evidence rather leaded to an alternative view of these areas.

Besides involvement of the lateral convexity of the left inferior frontal gyrus (IFG) in processing structural language features (Friederici, 2006; Friederici, Bahlmann, Heim, Schubotz, & Anwander, 2006; Grodzinsky, 2006; Grodzinsky & Friederici, 2006), it seems to be a universal processing device that plays a role in language and non-language tasks such as recognizing dependencies between related elements, detecting structural properties, movement preparation, and action recognition (e.g. Binkofski & Buccino, 2004; Decety et al., 1997; Hamzei et al., 2003; Tettamanti & Weniger, 2006; Thoenissen, Zilles, & Toni, 2002).

Neuroimaging studies also leave no doubt that regions in the (left) inferior frontal lobe outside the classically defined "Broca's area" – such as Brodmann area (BA) 47 and the ventral part of BA 6 – are essentially involved in the language processing network (Bookheimer, 2002; Devlin et al., 2003; Hagoort, 2005).

The classical model's receptive language center, the "Wernicke's area" proved to be similarly vaguely defined. The long-held belief that this region in the posterior part of the left perisyvian cortex is a speech-selective region (Bogen & Bogen, 1976; Wise et al., 2001; for a more detailed discussion see also Meyer, 2008) did not find support by insights from an

increasing number of neuropsychological and neuroimaging studies, which report different speech and non-speech related auditory functions to be correlated with activation in the posterior part of the left perisylvian cortex (e.g. Griffiths & Warren, 2002; Hickok & Poeppel, 2004; Wise et al., 2001).

In sharp contrast to assumptions generated by the classical model of language processing, evidence from neuroimaging studies show that listening to speech is correlated with bilateral and largely symmetrical activation of the superior temporal lobes (e.g. Hickok, 2009). Depending on the applied tasks and stimuli, studies found regions in the posterior (Hickok & Poeppel, 2007) or more anterior part of the superior temporal sulcus (STS) (Mazoyer et al., 1993; Narain et al., 2003; Scott, Blank, Rosen, & Wise, 2000; Spitsyna et al., 2006) to be involved in phonological processing stages. Anterior parts of the STS in particular have been found to be involved in sentence-level phonological processing, thus suggesting that the anterior part is responding to syntactic or prosodic organization of the stimuli (Hickok, 2009; Humphries, Binder, Medler, & Liebenthal, 2006; Humphries, Love, Swinney, & Hickok, 2005; Humphries, Willard, Buchsbaum, & Hickok, 2001; Vandenberghe, Nobre, & Price, 2002).

Furthermore, other extra-sylvian regions such as the middle temporal gyrus (MTG) (e.g. Turken & Dronkers, 2011) as well as subcortical areas (e.g. Kotz & Schwartze, 2010) were found to be essentially involved in language and speech processing.

As neuroimaging and increasingly sophisticated EEG and clinical studies provided much insight, different models of the functional anatomy of language – more or less closely related to the classical model – have been proposed (Poeppel, 2012; for an overview see also Ben Shalom & Poeppel, 2008). In particular, the apportionment of language into only two sub-components (production and comprehension) was criticized as being linguistically underspecified (Poeppel & Hickok, 2004) and thus dramatically neglecting the complexity and concepts of language, such as phonetics, syntax and semantics.

One approach of explicitly extending the classical model's focus on word-level processing has been presented by Friederici (2002). Her model is based on two major claims. The first addresses the question of functional anatomy and states that the temporal lobes subserve aspects of syntactic and semantic identification. The second claim is concerned with the order of syntactic and semantic processes. Friederici (2002) suggests that syntactic processing precedes semantic processing and both of them may interact during later stages of language processing (Ben Shalom & Poeppel, 2008). Moreover this model states the involvement of

"Broca's area" not only in language but also non-language sequences – such as the processing of musical sentences (Maess, Koelsch, Gunter, & Friederici, 2001). For the so-called "Wernicke's area" – considering only the posterior superior temporal cortex – the model proposes processes of identification of sub-lexical-phonological units and phonological word forms.

In an attempt to integrate neuropsychological, neuroimaging, and psycholinguistic data, Hickok and Poeppel (2004) presented a framework proposing dorsal and ventral streams in language processing, drawing on the model of cortical organization in the visual domain. For visual processing there exists the well-established idea of two substreams: a ventral "what" stream, projecting to the temporal lobe involved in visual object recognition and a dorsal "where" stream, projecting to the parietal and frontal lobes responsible for spatial visual processing (Mishkin & Ungerleider, 1982). Based on this model and earlier assumptions about dorsal-ventral partioning in the auditory system (Rauschecker, 1998), Hickok and Poeppel proposed that early cortical stages of speech perception involve auditory regions in bilateral superior temporal gyrus (STG), followed by a segmentation in a ventral stream involved in mapping sound onto meaning, and a dorsal stream, responsible for mapping sound onto articulatory-based representations (Hickok and Poeppel 2004, p. 72). While for the ventral stream the model predicts an involvement of the STS and the posterior inferior temporal lobe, including parts of the MTG and the inferior temporal gyrus (ITG), the dorsal stream is suggested to project toward the parietal lobe and ultimately to frontal regions (See Figure 2).

Giving a good overview of a possible language network including not only "traditional" language areas but also regions involved in working memory processes, this model has to be considered very broad in scope (Hickok & Poeppel, 2004). It does not, however, specify the essential involvement of frontal language systems and the role of subcortical regions, such as the basal ganglia and the cerebellum in language processing (Hickok & Poeppel, 2004; Kotz & Schwartze, 2010).

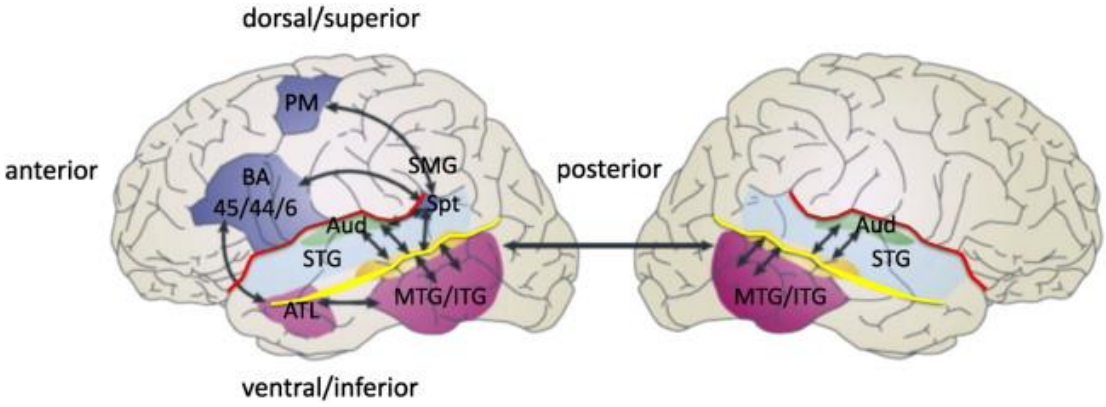

Figure 2. Dorsal and ventral streams of speech processing (Figure from Hickok & Poeppel, 2004).

In a recent review, Specht (2014) discusses emerging evidence for the dual-stream model, and suggests an expansion of the model by including brain areas repeatedly detected in neuroimaging studies of speech comprehension, namely the angular and the supramarginal gyrus (SMG) and subcortical areas like the basal ganglia, anterior insula, and cerebellum. He proposes the SMG to be at the intersection of the dorsal and ventral stream due to its involvement in categorical perception of phonological information as well as its relation to phonological working memory functions relevant for both streams (Specht, 2014).

Aiming to synthesize critical ideas of different models and to unify them in a more principled manner, thereby stepping away from a domain-specific view, Ben Shalom and Poeppel (2008) proposed a framework which is focused on three different aspects of language processing, namely memorizing, analyzing, and semantic synthesizing. Based on evidence from empirical studies, the model posits that the temporal lobe is particularly involved in memorizing processes in language perception with the suggestion of phonological processing located more dorsally, morpho-syntactic processing more in middle areas and retrieval of semantic representation in more ventral areas. Processes of analyzing are located in the parietal lobe, especially highlighting the role of the angular gyrus in conscious semantic decisions, and the SMG in conscious phonological decisions. Finally, the model emphasizes the role of the frontal lobe (BA 6, 44, 45, 47) in synthesizing between different elementary (phonological, lexical, semantic) items.

Additionally, Ben Shalom and Poeppel (2008) propose a superior to inferior gradient organizing the different aspect of computation. Hence across all lobes, phonological representations are suggested to be localized most superiorly, syntactic

information in the middle and semantic information most inferiorly. Still conceptualizing the anatomical distinction and involved linguistic operations quite coarsely, this model focuses on computations required to process language and can thus possibly account for findings in a less domain-specific manner.

To sum up, the plethora of studies concerning the neural basis of language and speech processing has contributed to an ever-increasing understanding of the likely contributions of certain brain regions and processing streams. But as Poeppel (2012) discusses, even a very sophisticated (linguistically and anatomically) model linking specific brain areas to a range of language phenomena does not provide explanations for underlying processes and functions.

Or as Poeppel (2012) states:

> "…a traditional quasimodular view (assigning phonology here, syntax there, etc.) cannot succeed, in part because the spatial studies suggest that much more fine-grained computational decomposition of linguistic domains into elementary representations and computations will be needed. " (Poeppel, 2012, pp. 38).

It therefore seems to be promising to follow a more parameter-based approach focusing on computational processes and thus to investigate how acoustic, linguistically relevant signals are encoded in order to process language and speech.

2. 2 Lateralization in speech processing

Having briefly outlined the history of cognitive neuroscience of language and speech processing, the topic of functional lateralization during speech (spoken language) processing will now be explicitly considered.

Since the insights of Broca, Wernicke and others (see Chapter 2.1), language processing has long been considered the almost exclusive domain of left-hemisphere auditory areas. Thus the role of the right hemisphere in language processing has been neglected by the classical model and was underestimated for a long time.

As mentioned above, with the advent of neuroimaging methods it became evident that also the right hemisphere is involved in speech processing (e.g Jung-Beeman, 2005; Meyer, 2008; Poeppel & Hickok, 2004; Ben Shalom & Poeppel, 2008). Decomposing language into subdomains and operations in more and more elaborate designs, the question of cerebral asymmetry became increasingly nuanced (Poeppel, 2012). Neuroimaging studies consistently reported bihemispheric involvement of perisylvian regions during speech perception (Hickok & Poeppel, 2000); and data from neuropsychological studies, particularly from patients with pure word deafness, hinted at an involvement of both hemispheres in speech perception (Poeppel, 2001). Poeppel (2001) notes:

> "(…)to date there exists no compelling evidence that, say, distinctive features, or morphemes, or roots, or phrasal types are selectively lateralized. Stored linguistic information may be encoded in various cortical regions in the left and right hemispheres, but the computations that operate over the putative representations appear to reflect lateralized specializations." (pp. 43).

As stated above, results of studies to date leave no doubt that speech perception is bilaterally mediated and that there exist hemispheric differences in the processing of speech information (Abrams, Nicol, Zecker, & Kraus, 2008; Boemio, Fromm, Braun, & Poeppel, 2005; Hickok, 2009; Hickok & Poeppel, 2007; Zatorre, Belin, & Penhune, 2002).

Speech signals contain a lot of acoustic information unfolding in time (Kotz & Schwartze, 2010) and acoustic information can be described at the time scale and frequency level. Spectrotemporal acoustic information and modulations form the basis of acoustic processing of auditory signals in general and thus processing of speech in particular.

Speech as a dynamically changing auditory signal contains critical information carried at multiple time scales (Poeppel, Emmorey, Hickok, & Pylkkänen, 2012). Therefore successful speech perception requires processing of different aspects of signals and relies upon intact time-resolution processes. While for instance information at intonation level is transferred at the scale of about 500-1000 ms, syllabic information is carried at 150-300 ms and rapidly changing features, such as voice onset times at around 20-80 ms (Poeppel et al., 2012). Thus changes of temporal information in speech generate events such as vowels, stressed or unstressed syllables and phrases (Kotz & Schwartze, 2010). Complementary information about pitch height, timbre, and tone are encoded through so-called spectral cues.

An often overlooked fact is that behavioral studies with healthy and brain-injured individuals reported a relationship between temporal characteristics of speech and cortical lateralization during speech perception decades ago (Efron, 1963; Schwartz & Tallal, 1980; Studdert-Kennedy & Shankweiler, 1970; Zurif & Mendelsohn, 1972).

During the last decade, the notion that the well-documented left hemispheric dominance for speech is a result of asymmetries in basic auditory processing has become increasingly supported.

Based on, among others, findings of an advantage of the left hemisphere for rapidly changing speech cues (Tallal, Miller, & Fitch, 1993) as well as an increased involvement of the right hemisphere in pitch processing (Binder et al., 1997; Griffiths, Johnsrude, Dean, & Green, 1999; Zatorre, Evans, & Meyer, 1994), Zatorre and Belin (2001) proposed a left-hemispheric specialization for rapid temporal processing, and a complementary sensitivity of the auditory regions of the right hemisphere for spectral auditory information. They supported their hypothesis with findings from a PET study where participants had to listen to pure tone patterns with systematically varied duration and frequency. While brain responses to the temporal features were lateralized towards the left hemisphere, responses to the spectral features were weighted towards the right superior temporal area (Zatorre & Belin, 2001).

A very similar approach has been chosen by Poeppel (2003) for his framework of the "asymmetric sampling in time*"* (AST) hypothesis, according to which functional asymmetries in speech perception and processing are based on different hemispheric preferences for temporal resolution (see Figure 3). While left auditory regions are suggested to be preferentially amenable to information in short temporal integration windows (~40 Hz), the right auditory cortex is stated to preferentially extract information over longer temporal integration windows (~4-10 Hz) (Poeppel, 2003). The model further posits that initial auditory processing in early stages of perception is occurring symmetrically in the left and right primary auditory cortices. Due to the temporal preferences of the cortical systems, speech is processed asymmetrically in following stages of analyses.

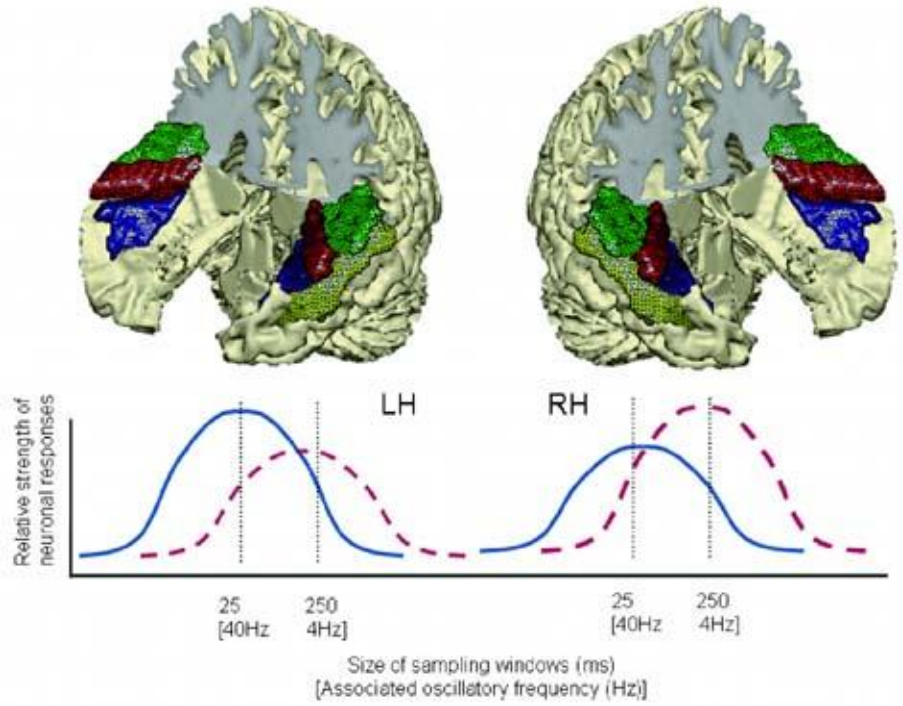

Figure 3. Functional asymmetries of computational preferences in the auditory-cortices (Figure from Meyer, 2008).

Concerning the contribution of the two hemispheres in speech processing, different predictions can be deduced from this framework. Firstly, given the fact that speech signals by nature contain fast and slow temporal features, neuroimaging studies using natural speech perception tasks should always yield bilateral activation. Secondly, the analysis of fast auditory cues should enhance left hemispheric activation, while slower formant transitions should lead to bilateral or even right-lateralized processing. Thirdly, processing at the level of intonation contour such as during prosody processing, should be related to enhanced right hemispheric involvement. Fourthly, and probably most interesting in the context of this thesis, Poeppel (2003) explicitly predicts a right hemispheric advantage in processing of phonetic phenomena at syllable-level.

Regarding the leftward preference for rapidly changing auditory and speech cues, the AST hypothesis has found support in a notable number of studies (Belin et al., 1998; Jamison et al., 2006; Jäncke, Wüstenberg, Scheich, & Heinze, 2002; Liégeois-Chauvel, de Graaf, Laguitton, & Chauvel, 1999; Schönwiesner, Rübsamen, & von Cramon, 2005; Schwartz & Tallal, 1980; Slevc, Martin, Hamilton, & Joanisse, 2011; Studdert-Kennedy & Shankweiler, 1970; Warrier et al., 2009; Zaehle, Jancke, Herrmann, & Meyer, 2009; Zaehle, Wüstenberg, Meyer, & Jäncke, 2004; Zatorre & Belin, 2001).

On the other hand, empirical evidence for the advantage of the right auditory-related cortex in processing slowly changing acoustic cues has been provided by a smaller number of studies. Nevertheless, the predictions of the models are in accordance with studies investigating processing of slowly fluctuating non-speech stimuli (Boemio et al., 2005), intonation contour, and speech melody (Meyer et al., 2002, 2004). Furthermore, evidence for increased right hemispheric involvement in suprasegmental domains of speech perceptions has been provided by studies investigating sentence rhythm (Geiser et al., 2008), and processing of rhythm and intonation in pseudo-speech (Zhang, Shu, Zhou, Wang, & Li, 2010).

It is important to emphasize that as a specific characteristic of the AST model it proposes continuous temporal scales (from 20 to 200 ms), rather than a discrete scale distinguishing between "short" and "long" temporal windows. Thus strongest evidence for the predictions of the model might come from studies incorporating a parametric design. Such neuroimaging studies that also employ longer natural speech stimuli (such as sentences) are very scarce (Liem, Hurschler, Jancke, & Meyer, 2014; McGettigan & Scott, 2012).

Liem et al. (2013) aimed to fill this gap by testing the predictions of the AST model in a recent fMRI study, employing spoken parametrically manipulated sentences as stimuli. According to a procedure introduced by Saberi and Perrott (1999), sentences were split into segments (of 100, 150, 200, and 250 ms) and locally time reversed. During scanning, participants had to perform a pattern-matching task. They first heard a sentence, followed by a probe stimulus and had to decide by button press whether or not the probe stimulus (time reversed) was a sample from the original version of the sentence. The results corroborate the predictions of the AST framework. While no functional lateralization in HG was found, they were able to show a shift to the right hemisphere in the PT and pSTG correlated with increasing time windows (longer probe segments). In addition, the correlation of hemodynamic response and task performance showed a tendency of an association between better task performance and functional rightward lateralization in the PT. In sum this study essentially contributes evidence to the validity of the AST model with regards to lateralization of suprasegmental speech processing.

2.3 Processes underlying auditory rhyme detection

As discussed above, speech signals contain information of different time scales, and temporal properties of speech appear to play an important role in functional cerebral lateralization. While analyses of rapid spectral changes occur in time windows of about 20-40 ms, suprasegmental cues such as syllabicity are processed in a time window of at least 100-200 ms (Rosen, 1992). Of particular interest in the context of this thesis is the longer time window whose processing the auditory related cortex of the right hemisphere has been proposed to be specialized in (Poeppel, 2003).

In the frame of this thesis we are particularly interested in the processing of syllables (and therefore the longer temporal time window) as important representational units in speech perception (Greenberg, 1998). Recently, the critical importance of syllable recognition in speech processing has received increasing attention.

The execution of a rhyme judgment and thus the decision that two words have a critical sound in common is closely related to the concept of phonological awareness, which can be broadly described as the sensitivity of sound units in words and the ability to manipulate them (Webb, Schwanenflugel, & Kim, 2004).

Typically, phonological awareness develops from awareness of rhymes and syllables to intrasyllabic units and phonemes (Goswami, 1993; Hoien, Lundberg, Stanovich, & Biaalid, 1995). The ability to detect rhyme is considered to be one of the earliest developing, most simple phonological awareness skills. A considerable amount of studies reported a foundational correlation between early phonological awareness and the development of early spelling and reading skills (e.g. Bradley & Bryant, 1983; Bryant, MacLean, Bradley, & Crossland, 1990; Stanovich & Cunningham, 1992). Therefore rhyming tasks are usually incorporated screening measures for the detection of early language and literacy acquisition difficulties (Wagensveld, van Alphen, Segers, Hagoort, & Verhoeven, 2013).

A task that is frequently used to test the extent of a person's ability to segment words into smaller phonetic units is spoken rhyme detection (e.g. "Which word does not rhyme: hat, cat, fish?) (Gillon, 2004). Generally speaking, rhyming means the relationship between two words or phonological compounds. A word that rhymes with "cat" is a word generated by altering the first phoneme and leaving the remaining phonemes the same (e.g. "hat") (Bower & Bolton, 1969). Therefore, in order to decide whether or not two syllables in spoken sentences rhyme, listeners have to identify the critical syllable of a prime word, to store it in

phonological memory, to possibly articulatory rehearse it, and finally to compare it to another segmented rhyme unit.

However, there is some controversy concerning the phonological operations behind rhyme detection in two words. While it has been argued that the ability to detect rhyme involves more or less conscious analytical processes of segmenting the so-called *rime*[1] unit from the critical words (see Figure 4) and to compare them (Bradley & Bryant, 1983), others argue for a more general ability to detect global phonological similarity (Cardoso-Martins, 1994).

It is important to consider the tasks used to measure rhyme detection skills. Many studies use explicit rhyme detection on either (short) words or pseudowords. Wagensveld et al. (2012) discuss the observation that more demanding rhyme decision tasks (e.g. including phonological distractors) influence rhyme performance (Cardoso-Martins, 1994). Wagensveld et al. (2012) investigated the influence of task demands on rhyme detection in children by presenting the subjects with a word and a pseudoword rhyming task including phonological distractors. They reported poorer performance for pseudowords and phonologically overlapping non-rhyming pairs. The difference of this so-called "global similarity effect" between the word and non-word rhyme condition lead them to the conclusion that rhyme judgments are neither purely based on global phonological overlap nor solely resulting from analytic processing. Rather they propose a combination of these theories to explain how children make rhyme judgments. Their results emphasize the importance of more demanding rhyme conditions in order to measure rhyme detection in more detail.

By introducing rhyming paradigms with sentences, and by using pseudowords instead of real words, demands on segmentation processes are clearly enhanced (Wagensveld et al., 2012). Rhyme judgments in sentences further require keeping phonetic information active until the second critical syllable is encountered – a process that is strongly believed to involve working memory. According to Baddeley's influential model (Baddeley, 2003), verbal working memory can be divided into a subvocal rehearsal system and a phonological store. While the former is suggested to be able to store verbal (auditory) information for a short period of time, the latter is supposed to be responsible for the maintenance of the information held in the phonological store (Baldo & Dronkers, 2006). Rhyme judgments are stated to involve both of these processes (Baddeley, Lewis, & Valler, 1984; Besner, 1987).

[1] The term „rhyme" is used in the context of judgments about phonology (as in the rhyme detection tasks used in the studies) and in a general way to describe the phonological unit of any word following the first consonant (onset). On the contrary the term "rime" is used in the case that the phonological unit refers specifically to a single syllable (Ziegler and Goswami, 2005, p.4)

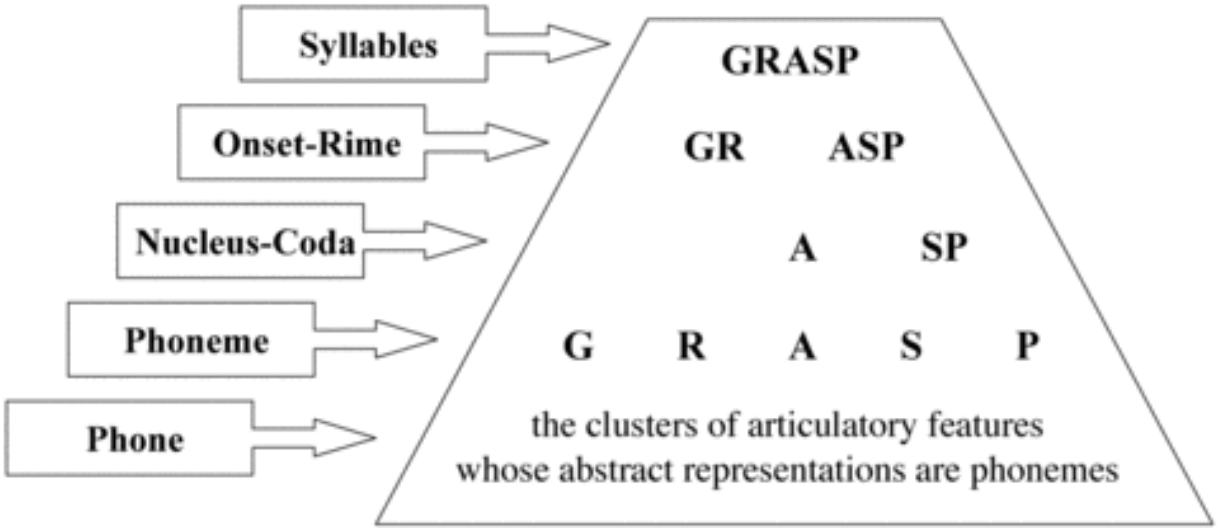

Figure 4. Depiction of different phonological grain sizes (Figure from Ziegler and Goswami, 2005)

2.4 State of research on neural basis of auditory rhyme processing

To date, rhyme processing has predominantly been investigated by EEG studies and almost exclusively used pairs of words and nonwords as stimuli. Based on an event-related potential (ERP) study, Rugg et al. (1984b) was the first to report the neural correlate of rhyme processing as a right lateralized increased negative deflection for non-rhyming as compared to rhyming words around 450 ms after target onset. In a subsequent study, it could be showed that this effect was equally induced by non-rhyming nonwords (Rugg, 1984a) and thus the modulation of the N450 component apparently was not linked to semantic processes. Since then the N450 effect could be shown in many studies using different stimuli such as single letters (Coch, Hart, & Mitra, 2008) or multi-syllabic pseudowords (Dumay et al., 2001).

However, it has been proposed that the N450 component is not specifically reflecting rhyme matching but rather a general sensitivity to phonological overlap (Perrin & García-Larrea, 2003; Praamstra, Meyer, & Levelt, 1994; Radeau, Besson, Fonteneau, & Castro, 1998). The fact that this effect is also found when targets are spoken in a different voice than primes, suggests that this rhyming effect is an index of phonological processing rather than simply for a physical-acoustic mismatch (Praamstra & Stegeman, 1993).

In addition to the more negative bilateral posterior response for nonrhyming targets (Rugg, 1984a), Khateb et al. (2007) reported rhyme-specific response, expressed by a more negative response at lateral sites for rhyming targets (Coch, Grossi, Skendzel, & Neville, 2005; Khateb et al., 2007) before the N450 component. However, the fact that these EEG studies were at word rather than at sentence level and considering the different temporal and spatial resolutions of EEG and fMRI, limits their informative value for the present work.

As mentioned before, neuroimaging studies on auditory rhyme processing are very scarce and the vast majority of existing functional imaging studies concerning the neural substrate of rhyme processing used written stimuli (e.g. Paulesu, Frith, & Frackowiak, 1993; Pugh et al., 1996; Sergent, Zuck, Lévesque, & MacDonald, 1992). Typically these studies with words and/or pseudowords found inferior frontal activation during rhyme processing, and it has been argued that this frontal activation is linked to the recoding of spelling information to sound (Fiez, Balota, Raichle, & Petersen, 1999; Herbster, Mintun, Nebes, & Becker, 1997).

So far, only a handful of neuroimaging studies have investigated auditory rhyming processing (e.g. Burton, Locasto, Krebs-Noble, & Gullapalli, 2005; Rumsey et al., 1992). Most of them used single words or syllables and often included dyslectic adults (Hernandez et al., 2013) or children (Kovelman et al., 2012) as subjects. A relatively consistent finding of these studies is increased activation in the left IFG and bilateral STG associated with the performance of a rhyme judgment task in healthy subjects (Booth et al., 2002; Booth et al., 2004; Burton et al., 2005; Kovelman et al., 2012). Booth et al. (2004) showed that adults as well as children activate the left IFG, bilateral superior and middle temporal gyri, as well as the left fusiform gyrus during auditory rhyme decision.

2.5 Methods

As mentioned above, for a long time our knowledge of the cerebral basis of language processing was mainly based on clinical reports on associations of a brain-damaged site with specific loss of language and speech functions. With the advent of computer tomography in 1973 and in particular the development of functional neuroimaging techniques, such as functional magnetic resonance imaging (fMRI) and positron emissions tomography (PET), a paradigmatic change has been brought about, allowing noninvasive ‘in vivo’ observation of the brain. Below the basic principles of the used methodology in the empirical part of this thesis are briefly sketched. Specific parameters as well as detailed information on the

experimental procedures applied during fMRI sessions and analysis of data are described in the corresponding parts of the original research articles (see Chapter 4).

2.5.1 Principles of functional magnetic resonance imaging (fMRI)

By means of fMRI, neural activity is commonly mapped by measuring the blood-oxygen-level-dependent (BOLD) signal change. This hemodynamic signal change is indirectly measured due to local changes in magnetic fields while performing a task. The physiological basis of the BOLD signal lies in the fact that neural activity leads to a rise in regional cerebral blood flow thus changing the local ratio of paramagnetic oxyhemoglobin and diamagnetic deoxyhemoglobin. Neural activation in a specific region leads to the consumption of oxygen and therefore to an initial dip in the measured hemodynamic response. After this initial decrease of oxyhemoglobin, there is overcompensation due to an increase of cerebral blood flow with oxygenated hemoglobin leading to an increase in the measurable MR-signal (Ogawa et al., 1993; Ogawa, Lee, Kay, & Tank, 1990). Figure 5 shows the typical time-course of the BOLD signal with the initial dip directly after stimulation, followed by a signal intensity rise and a maximal reaction after about 4-6 seconds (Jäncke, 2005).

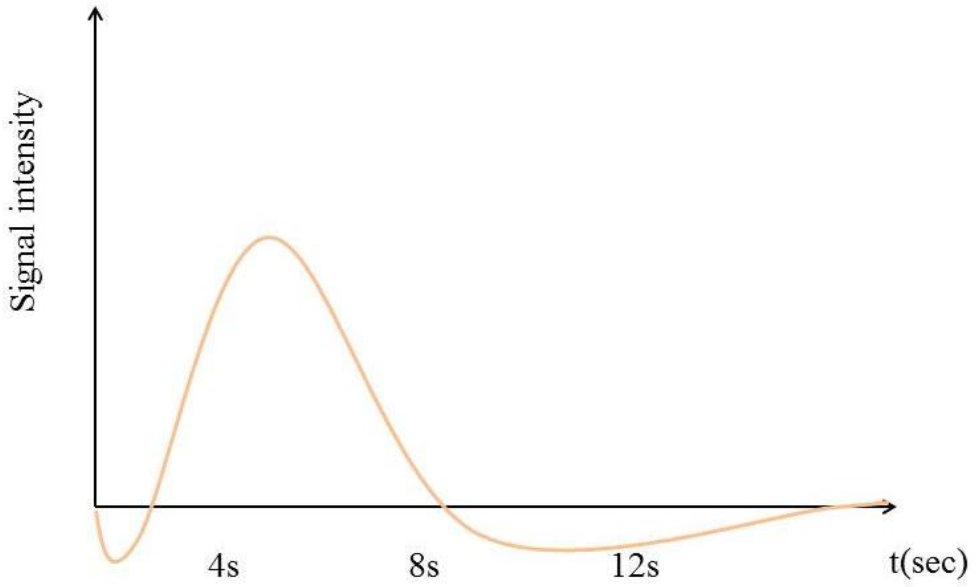

Figure 5. Time-course of the BOLD signal, showing the initial dip, followed by an increase of measurable signal and a maximal reaction after about four seconds.

Research has been able to show a strong correlation of the BOLD signal with local field potentials (Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001) and therefore counts as a valid measure of neural activity (Logothetis, 2003; Logothetis, 2008). By this method, three dimensional functional maps of the brain with a relatively high spatial resolution (approximately 2-3 mm) are produced (Jäncke, 2005).

2.5.2 Clustered-sparse acquisition

To record the above-described MR-signal during a task, participants are placed in a scanner that produces a strong permanent magnetic field. In order to be able to measure differential magnetic responses of oxygenated and deoxygenated hemoglobin, additional magnetic fields (gradients) and radiofrequency pulses are applied. The switch of the gradient coils can lead to acoustic noise reaching levels up to 130 dB. This noise brings about a variety of problems, particularly in the context of auditory imaging studies (Amaro et al., 2002; Moelker & Pattynama, 2003). Not only does the overlap between the scanner noise and the auditory stimulus presentation hamper the perception of the stimuli but the perception of an auditory stimulus in an obscuring acoustic background can also increase attentional demands, which in turn might provoke additional functional responses in extra-auditory frontal areas (Schmidt et al., 2008). Moreover, auditory scanner noise can lead to saturation of auditory neurons and thus the noise per se induces BOLD responses in auditory-related brain regions during trials lacking auditory stimulation. This additional input can lead to a reduction in the possible range of stimulus-induced BOLD response (Gaab, Gabrieli, & Glover, 2007).

To overcome these problems, techniques have been developed and are now frequently used in auditory fMRI studies (Eden, Joseph, Brown, Brown, & Zeffiro, 1999; Hall et al., 1999).

By means of a so-called “sparse” acquisition technique, the influence of acoustical scanner noise is successfully reduced (Amaro et al., 2002; Hall et al., 1999). Due to an enhancement of the interval between single volume scans, this acquisition scheme allows the insertion of silent intervals between image acquisitions, during which auditory stimuli are presented (Schmidt et al., 2008).

Compared to continuous scanning it could be shown that this technique allows for the localization of functional activation with enhanced spatial and functional specificity (Yang et al., 2000), but it has the disadvantage of requiring longer total scanning duration in order to collect sufficient data for powerful statistical analyses (Schmidt et al., 2008). This problem

has been minimized by the introduction of an extension of this design, the so-called "clustered-sparse" design.

In order to combine advantages of the "silent" sparse acquisition technique with more time-efficient data collection, in such a clustered-sparse design multiple scans are acquired in rapid succession after each trial (Schmidt et al. 2008). Meanwhile, such schemes have been successfully employed in a variety of auditory studies (Di Salle et al., 2001; Liem, Lutz, Luechinger, Jäncke, & Meyer, 2012; Schwarzbauer, Davis, Rodd, & Johnsrude, 2006; Zaehle, et al., 2004).

In a recent methodological study, Liem et al. (2012) investigated the influence of different cluster-onset asynchronies on effect sizes and reported that a protocol including a short cluster-onset asynchrony (7.5 s) led to more advantageous results than protocols with longer cluster-onset asynchronies, due to the possibility of an increased amount of stimuli presentation in a given period of time.

3. AIMS AND RESEARCH QUESTIONS

The principal purpose of this thesis is to investigate the neural basis of auditory rhyme detection at sentence-level. The main motivation for this aim is twofold:

Firstly, despite the theoretical and practical importance of rhyme in the context of language learning and language lateralization, studies investigating the neural basis of auditory rhyme processing are very scarce. Over the past decades rhyme processing has predominately been investigated using real word stimuli or syllables that were visually presented (e.g. Paulesu, Frith, & Frackowiak, 1993; Pugh et al., 1996). Since studies using visual stimuli including nonwords (Pugh et al., 1996; Xu et al., 2001) and real words (Crosson et al., 1999; Kareken, Lowe, Chen, Lurito, & Mathews, 2000; Xu et al., 2001) require cross-modal transfer processes, they are difficult to compare to rhyming studies in the auditory modality.

Given the fact that rhyme detection generally seems to be closely related to the development of different language skills and the ability to detect rhyme in pre-school significantly correlates with later success in learning to read and write (Bryant, Bradley, MacLean, & Crossland, 1989), it has to be considered a research gap that there exists hardly any knowledge of the neural network underlying successful rhyme detection in general.

Secondly, the investigation of neural correlates of sentence-level rhyme processing is theoretically suggested to contribute to a better understanding of right-hemispheric contribution during speech processing. As stated before (see Chapter 2.2), the AST model (Poeppel, 2003) explains and predicts lateralization during speech processing based on differential specializations of the auditory cortices of the two hemispheres for processing temporal speech cues. The model states an initial symmetrical representation of the speech signal in primary auditory cortices of both hemispheres, followed by a lateralized pattern of activation in non-primary auditory regions. While the left temporal region is suggested to be especially amenable for rapidly changing acoustic features, the right auditory-related region is suggested to be preferentially driven by the processing of slowly changing cues. Poeppel (2003) predicts a rightward lateralization during speech tasks relying on segmentation processes that require segmentation into syllables. Considering the processes underlying successful rhyme judgments, such a task should be associated with enhanced activation of the auditory related cortex of the right hemisphere.

Thus by means of two fMRI studies this thesis aims to further investigate the neuroanatomical regions and the presumed lateralized activation of these regions involved in auditory rhyme processing.

Both empirical studies use pseudo-sentences as stimuli, thus laying the focus on phonological processing and ruling out conscious semantic processes at its best. By employing fMRI technique (see chapter 2.5.2), we employed a method with high spatial resolution, which permitted us to identify brain regions involved in sentence-level rhyme detection in a general sense. The clustered-sparse acquisition scheme allowed us to present stimuli during silence and thereby to avoid the negative implication of the scanner noise.

The first study is – to our knowledge – the first fMRI study investigating the cortical correlates of auditory rhyme processing at sentence-level. In an auditory clustered-sparse fMRI design, 22 healthy subjects were required to fulfill an explicit rhyme detection task. This study therefore aimed at gaining a first insight in neural processes underlying rhyme detection in sentential context. By using "meaningless" pseudo-sentences and keeping the distance between the critical syllables constant through a metrical stress pattern, focus has been set to the explicit detection of rhyme.

The second fMRI study was designed to build on the findings of the first explorative study. By adapting the paradigm, cognitive demands of the task were increased. The 14 subjects had to listen to pseudo-sentences[2] that varied in the presence of rhyme and regular meter. After the presentation of the stimuli they were asked to either fulfill a rhyme or a meter detection task. In addition to the further investigation of neural processing underlying the performance of a rhyme detection task, the purpose of this study was to investigate the influence of metrics on rhyme perception and thus to examine the neural correlates of the interaction of rhyme and (regular) meter.

To sum up, the studies have been designed to answer the following research questions:

Research question 1:

What are the basic neural correlates of auditory rhyme processing at sentence-level?

Based on the processes involved in successful auditory rhyme detection and previous studies on (word-level) rhyme detection, we expect to find bilateral activation in auditory related

[2] Note: In the publication of the second study the stimuli are called „versed word strings" due to a reviewer's comment. Within this thesis, the two terms (pseudo-sentences and versed word strings) are used interchangeably.

cortices as well involvement of regions linked to working memory, such as the SMG and the IFG.

Research question 2:

How are these processes of auditory rhyme detection influenced by the metrics of the stimuli?

Due to the lack of pertinent research, this question has to be addressed in an exploratory way. We expect neural responses to rhyme detections to be modulated by the presence (or absence) of metrics.

Research question 3:

Does sentence-level rhyme detection lead to increased activation of right hemispheric auditory related regions?

Based on assumptions of the parameter-based "asymmetric sampling in time" framework (Poeppel, 2003), we expect to find a rightward lateralization in secondary auditory regions (posterior STS) associated with an auditory rhyme detection task.

4. EMPIRICAL PART

4.1 **Study I:** Right and left perisylvian cortex and left inferior frontal cortex mediate sentence-level rhyme detection in spoken language as revealed by sparse fMRI

Authors:

Martina A. Hurschler[1,2§], Franziskus Liem[1,2], Lutz Jäncke[1,2,3], and Martin Meyer[2,3,4]

[1]Univ Zurich, Inst Psychol, Div Neuropsychol, CH-8050 Zurich, Switzerland
[2]Univ Zurich, Inst Psychol, Neuroplasticity and Learning in the Healthy Aging Brain (HAB LAB), CH-8006 Zurich, Switzerland
[3]International Normal Aging and Plasticity Imaging Center, University of Zurich, Switzerland
[4]Center for Integrative Human Physiology, University of Zurich, Switzerland

Published 2013 in: Human Brain Mapping 34: 3182-3192.

Acknowledgements:

The authors acknowledge ongoing research support from the Swiss National Science Foundation (Grants 320030-120661 to MM), the 'Fonds zur Forderung des akademischen Nachwuchses' (FAN), and the 'Zurcher Universitatsvereins (ZUNIV). We express our gratitude to Sarah McCourt Meyer and two anonymous reviewers for helpful comments on an earlier draft.

4.1.1 Abstract

In the present study we used functional magnetic resonance imaging (fMRI) to investigate the neural basis of auditory rhyme processing on sentence level in healthy adults. In an explicit rhyme detection task participants were required to decide whether the ending syllable of a metrically spoken pseudo-sentence rhymed or not. The performance of this task revealed bilateral activation in superior posterior temporal gyri with a much more extended cluster of activation in the right hemisphere.

The direct contrast between rhymed and non-rhymed trials revealed a stronger BOLD response for rhymed trials in the frontal operculum and the anterior insula of the left hemisphere. Our results suggest an involvement of these frontal regions not only in articulatory rehearsal processes, but also in the detection of a matching syllable, as well as in the execution of rhyme judgment. These findings suggest that the right hemisphere supports suprasegmental tasks, such as, the segmentation of speech into syllables. In conclusion, our results are in line with the "asymmetric sampling in time" model suggested by Poeppel (2003).

4.1.2 Introduction

The ability to detect rhyme is considered to be one of the earliest developing and most simple phonological awareness skills (Coch, Mitra, George, & Berger, 2011). The sensitivity to spoken rhyme has previously been linked to the development of different language functions, such as, reading and spelling. Nevertheless, barely any neuroimaging studies about the neural correlates of auditory rhyme processing exist today.

Young children appear to appreciate rhyme (Bryant et al., 1989) and there is evidence that they are able to fulfill rhyme detection tasks as early as 3-year-old (Stanovich, Cunningham, & Cramer, 1984). Hence, children seem to ascertain rhyme in spoken language before they have reached the ability to detect phonetic segments. This observation is consistent with the linguistic status hypothesis, which maintains that syllables have an advantage over intrasyllabic units and that intrasyllabic units, in turn, have an advantage over individual phonemes (Treiman & Kessler, 1995).

Numerous behavioral longitudinal and crosscultural studies have been able to show that preschool experiences with auditory rhyme detection have a significant effect on later success

in learning to read and write (Bryant et al., 1989). Both sensitivity to spoken rhyme and measures for memory span are related to vocabulary development in preschoolers (Avons, Wragg, Cupples, & Lovegrove, 1998).

With respect to the neural correlates of auditory rhyme processing, evidence is currently sparse. Speech perception relies on mechanisms of time-resolution at a time scale level of milliseconds. The predominance of the left perisylvian region for most domains within speech processing is an evidenced fact in neuroscientific research (e.g. Brunswick, McCrory, Price, Frith, & Frith, 1999; Friederici, 2011; Narain et al., 2003; Price, 2000; Vigneau et al., 2006; Vigneau et al., 2011). Following the traditional model of language, the majority of colleagues, who do research in aphasia, emphasize the superior and cardinal role of the left hemisphere. Clinical literature has often reported sensory aphasic problems resulting from left temporal lobe lesions (e.g. Kuest & Karbe, 2002; Turner, Kenyon, Trojanowski, Gonatas, & Grossman, 1996). This left perisylvian region is the site for both elemental functions, such as, phonetic processing, and higher purposes, namely, syntactic and semantic detection. However, gradually mounting evidence obtained from neuroimaging studies in non brain-damaged individuals proposes that the contribution of the right hemisphere to the processing of speech perception must not be underestimated (Jung-Beeman, 2005; Meyer, 2008; Poeppel & Hickok, 2004; Ben Shalom & Poeppel, 2008; Stowe, Haverkort, & Zwarts, 2005; Vigneau et al., 2011).

In the current study we investigate the neural signatures of auditory rhyme processing at the sentence level because we believe that learning more about this issue will contribute to the topic of functional lateralization in speech processing. This assumption is based on the very nature of different processes that are involved in the performance of an auditory rhyme detection task, such as, the automatic registration of phonological input, the processing of phonemic segmentation, the retention of information in the articulatory loop, the comparison of critical word-ending sounds, and both decision making and response provision (Baddeley et al., 1984). As regards the suprasegmental processes, which form the basis of rhyme detection, one might predict a right-lateralized activation in the posterior–superior temporal gyrus (pSTG) as suggested by the “asymmetric sampling in time” (AST) hypothesis proposed by Poeppel (2003). According to this framework, auditory information is preferentially integrated in differential temporal windows by the nonprimary auditory fields residing in the two hemispheres. While the left hemisphere is suggested to be specialized for the perception of rapidly changing acoustic cues (~40 Hz), this model predicts a better adaption of the right auditory cortex for slowly changing acoustic modulations (~4 Hz).

In support of the "AST"-hypothesis, different studies were able to demonstrate that the right supratemporal plane is especially amenable to slow acoustic modulations in speech (Hesling, Clément, Bordessoules, & Allard, 2005; Ischebeck, Friederici, & Alter, 2008; Plante, Creusere, & Sabin, 2002; Zhang et al., 2010). In particular, activation in the posterior supratemporal region of the right hemisphere was associated with speech melody processing (Gandour et al., 2004; Meyer et al., 2002, 2004) and explicit processing of speech rhythm (Geiser et al., 2008).

According to Poeppel (2003), the AST model permits different predictions regarding the lateralization of different speech perception tasks. One such prediction states that "phonetic phenomena occurring at the level of syllables should be more strongly driven by right hemisphere mechanisms" (Poeppel, 2003, p. 251). The problem with investigating this assumption is that syllables always contain their phonemic constituents (Poeppel, 2003). Therefore, an insightful experiment should disentangle selective processing of syllables from the more general processing of their constituent phonemes. This reasoning has found some support by a dichotic listening study that showed increased rightward lateralization when the focus of the task emphasized syllabicity instead of the phonemic structure of the stimuli (Meinschaefer, Hausmann, & Güntürkün, 1999).

We believe, that akin to speech meter, rhymes serve as structural devices. Geiser et al. (2008) have previously investigated the neural correlates of explicit rhythm processing in spoken sentences by using German pseudo-sentences spoken in either an isochronous, or a conversational rhythm. In the explicit task, subjects had to judge, whether the heard pseudo-sentence was "isochronous" or "nonisochronous" (rhythm task) that is whether the sentence had a metrical structure or not. In the implicit condition, unattended rhythm processing was measured, while participants had to decide, whether the sentence they heard was a question or a statement (prosody task). One particular result that they provided is increased rightward lateralization in temporal and frontal regions associated with explicit processing of speech rhythm. Interestingly, they did not find this right lateralized temporal activation in the implicit stimulus-driven processing condition. The observed difference in activation between implicit and explicit condition is in line with previous auditory functional imaging studies that were able to demonstrate task-dependent modulation of auditory cortical areas involved in speech processing (Noesselt, Shah, & Jäncke, 2003; Poeppel et al., 1996; Scheich, Brechmann, Brosch, Budinger, & Ohl, 2007; Tervaniemi & Hugdahl, 2003).

The task used in our study resembles the explicit task used in the study by Geiser et al. (2008) insofar as the focus of subjects' attention is explicitly set to suprasegmental analysis. Based on the aforementioned findings, we hypothesize that an explicit rhyme detection task at the sentence level should be associated with increased involvement of the right perisylvian cortex.

With respect to the direct comparison between rhymed and nonrhymed stimuli we have to consider cognitive demands that may be involved. To accurately perform a rhyme detection task, the phonetic information should not only be segmented into syllables; indeed, it should also be memorized until the critical phoneme is encountered. The distance between the two relevant phonemes involves working memory (WM), as one item must be kept active until it can be compared with a second phonetic element. According to Baddeley's influential model, verbal memory is thought to be divided by a subvocal rehearsal system and a phonological store. While the phonological store is suggested to hold auditory/verbal information for a very short period of time, articulatory rehearsal is a more active process that retains the information in the phonological store (Baldo & Dronkers, 2006).

It has been previously argued that rhyme judgments engage both of these processes (Baddeley et al., 1984). Several PET and functional magnetic resonance imaging (fMRI) studies that used 2-back or 3-back tasks to investigate WM found activation in the left IFG (mostly in the opercular part, corresponding FOP; see Rogalsky & Hickok, 2011; Tzourio-Mazoyer et al., 2002), which was related to articulatory rehearsal. In addition, it has been proposed that the left IPL subserves the phonological store (Paulesu et al., 1993).

Contrary to most of the previous studies about rhyme processing, we used pseudo-sentences instead of real word stimuli. Therefore, we are able to rule out possible confounds brought about by obvious semantic processing. To control for WM load, the pseudo-sentences were spoken metrically. This enables the span between the end rhymes to remain constant. To direct the participants' attention to the phonology stimuli's last syllable, all of the pseudo-sentences were spoken in the same isochronous rhythm.

As previously mentioned, explicit rhyme detection at the sentence level has not yet been investigated with fMRI methodology. Based on the predictions of the AST hypothesis, as well as findings from the aforementioned studies pertaining to prosody and speech meter, we predict that the rhyme detection task per se should be related to enhanced supratemporal recruitment of the right auditory-related cortex. Because of the cognitive demands of the task used, we also expect the recruitment of areas related to the phonological loop of the WM, such as, the left inferior parietal lobe and the (left) frontal operculum.

Since our approach investigates hemispheric lateralization in processing acoustic suprasyllabic spoken language, we further explore the division of labor between the right and the left auditory-related cortex. The goal of this study is to investigate neural signatures of auditory rhyme detection at the sentence level. This should not only enhance the understanding of the neural processes underlying the detection of rhyme in rhymed (metrical) sentences, but also the relationship between slowly changing acoustic modulations and right auditory-related cortex functions in general.

4.1.3 Methods

Subjects

A total of 22 healthy subjects (11 females) aged 19 - 31 years (mean=23.5, SD=3.6) participated in this study. According to the Annett-Handedness-Questionnaire (AHQ) (Annett, 1970) all subjects were consistently right-handed. They were native speakers of (Swiss) German with no history of neurological, major medical, psychiatric, or hearing disorders. All subjects gave written consent in accordance with procedures approved by the local Ethics Committee. Subjects were paid for their participation.

Stimuli

Stimuli material comprised a total of 72 pseudo-sentences containing phonotactically legal pseudowords. Our stimuli resemble so-called “jabberwocky” sentences used in prior studies (Friederici, Meyer, & von Cramon, 2000; Hahne & Jescheniak, 2001) in that, they contain some real German function words. In contrast with typical jabberwocky sentences, they display a regular meter and do not contain systematic morphological markers, in order to minimize semantic and syntactic associations. Rhymed and non-rhymed sentences were matched based on the amount of function words they contained.

The last syllable of the stimuli either rhymed (R) or did not rhyme (NR) with the last syllable of the first part of the sentence (See Figure 6). The pseudo-sentences were metrically spoken by a trained female speaker and consisted of a verse form, which means that sentences followed a regular meter (eight iambs per sentence). As a result, each pseudo-sentence contained 16 syllables and the sentences consisted of a mean of 10.4 pseudowords (SD±1.4).

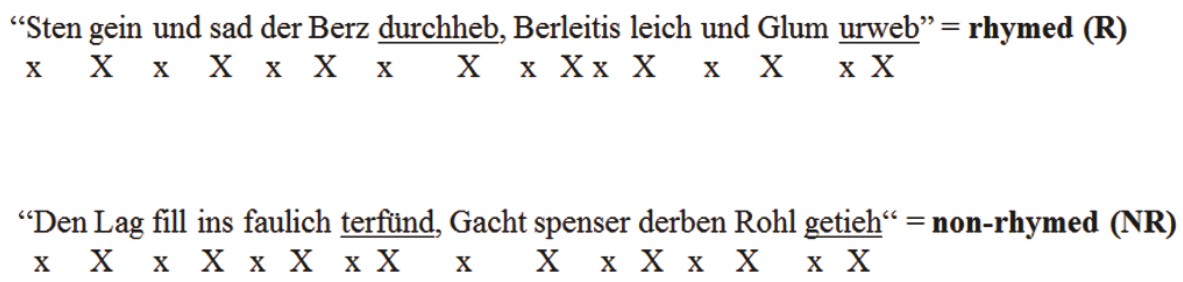

Figure 6. Examples of pseudo-sentences. Underlined are the pseudowords that had to be compared.

All stimulus items were normalized in amplitude to 70% of the loudest signal in a stimulus item. All pseudo-sentences were analyzed by the means of PRAAT speech editor (Boersma, 2001). Stimuli were balanced with respect to mean intensity, and the length of all stimuli was set to exactly 6 s.

Task/Procedure

Each participant read instructions to the experiment, gave their written consent, and completed the Annett-Handedness-Questionnaire.

During scanning, the room lights were dimmed and a fixation cross was projected, via a forward projection system, onto a translucent screen placed at the supine position at the end of the magnet's gurney. Subjects viewed the screen through a mirror attached to the head coil. Stimuli were presented using Presentation® software (Version 0.70, www.neurobs.com). The stimulus presentation was synchronized with the data acquisition by employing a 5 V TTL trigger pulse. We used an MR-compatible piezoelectric auditory stimulation system that is incorporated into standard Philips headphones for binaural stimulus delivery.

Subjects were instructed to decide as quickly and as accurately as possible whether the pseudo-sentences that they were presented with rhymed or not. They indicated their response by pressing a button on the response box with either their right index finger, or with their right middle finger. Additionally, a total of ten null events were created to be a baseline condition and were randomly included in the time course of the experiment. During the empty trials, subjects were instructed to press a random button. In one run, a total of 82 trials (36 rhymed pseudo-sentences, 36 non-rhymed pseudo-sentences, and 10 empty trials) were presented. A

fixation cross was presented for 500 milliseconds prior to each stimulus presentation. The task in the scanner lasted 20 min 30 s.

Data Acquisition

The functional imaging study was performed on a Philips 3T Achieva whole-body MR unit (Philips Medical System, Best, The Netherlands) equipped with an eight-channeled Philips SENSE head coil. In order to acquire data, a clustered sparse temporal acquisition technique was used. This scheme combines the principles of a sparse temporal acquisition with a clustered acquisition (Liem et al., 2012; Schmidt et al., 2008; Zaehle et al., 2007). That way, the stimuli were binaurally presented in an interval devoid of auditory scanner noise. Three consecutive volumes were collected, in order to cover the peak of the event-related hemodynamic signal (See Figure 7).

Functional time series were collected from 16 transverse slices covering the entire perisylvian cortex with a spatial resolution of 2.7 x 2.7 x 4 mm^3 by using a Sensitivity Encoded (SENSE) (Pruessmann, Weiger, Scheidegger, & Boesiger, 1999) single-shot, gradient-echo planar sequence (acquisition matrix 80x80 Voxels, SENSE accelerator factor R=2, FOV= 220 mm, TE =35 ms). The volumes were acquired with an acquisition time of 1000 ms each, a flip angle = 68°, and a 12 sec intercluster interval was employed; as a result, one trial lasted 15 seconds. Furthermore, a standard 3-D T1 weighted volume for anatomical reference was collected with a gradient echo sequence with a 0.94x0.94x1 mm spatial resolution (160 axial slices, acquisition matrix 256x256 voxels, FOV=240 x 240 mm, repetition time [TR] = 8.17 ms, flip angle=8°).

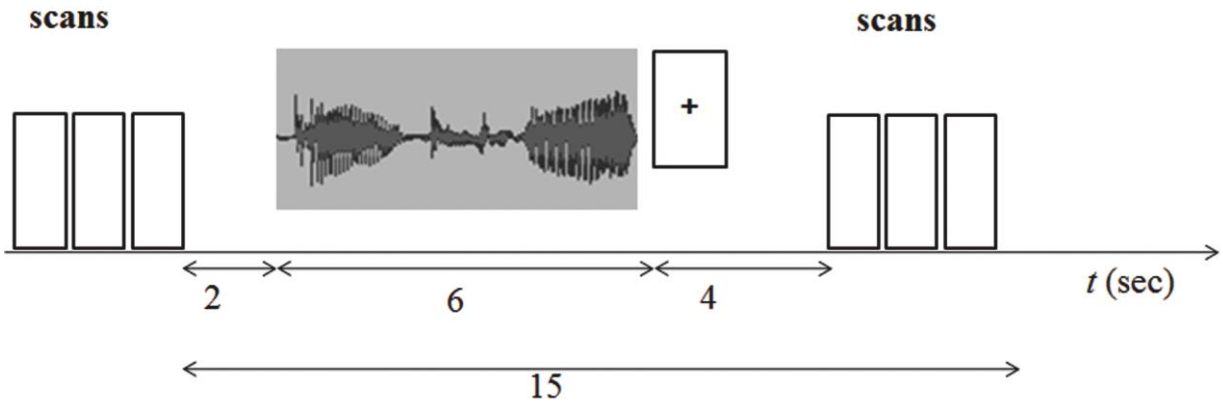

Figure 7. Acquisition scheme. Depicted are the three time points of acquisition and the stimulus presentation in one trial.

Data Analysis

Behavioral data analysis and ROI statistics were performed by using SPSS Statistics 19.0 (SPSS Inc.).

Behavioral Data

During the experiment in the scanner, behavioral performance data on the rhyme detection task were collected. Data (reaction time and accuracy) were corrected for outliers (>2 S.D. above or below mean value). A repeated-measures t-test was performed to identify significant differences between the conditions.

fMRI analysis

Artifact elimination and image analysis was performed by using MATLAB 7.4 (Mathworks, Natick, MA) and the SPM5 software package (Institute of Neurology, London, UK; http://www.fil.ion.ucl.ac.uk). In order to account for movement artifacts, all volumes were realigned to the first volume, normalized into standard stereotactic space (voxel size 2x2x2 mm^3, template provided by the Montreal Neurological Institute), and smoothed using a Gaussian kernel with a 6 mm full-width-at-half-maximum that increased the signal-to-noise ratio of the images. Due to the low number of sampling points, a boxcar function (first order, window length=3sec) was modeled for each trial. In addition, two regressors of no interest were included, in order to account for the T1-decay along the three volumes (Liem et al., 2012; Zaehle et al., 2007). The resulting contrast images from each of the first level fixed-effects analysis were entered into one-sample t-tests (df=21); thereby, permitting inferences about condition effects across subjects (Friston, Zarahn, Josephs, Henson, & Dale, 1999). Unless otherwise indicated, regions reported showed significant effects of $p<0.05$ and were FWE corrected.

Post-hoc region of interest analyses

To statistically test for asymmetry in cluster size of temporal activation, cluster sizes in the right and the left STG at the single-subject level ($p<0.001$, unc.) were extracted via an in-house-tool and subjected to a 2x2 repeated-measures ANOVA with the factors *condition* and *hemisphere*, followed by paired t-tests with the cluster extent in the right and the left STG for both conditions.

4.1.4 Results

Behavioral data

Individual mean reaction times (RT), as well as accuracy scores were distributed normally in both the R and the NR conditions (Kolmogorov-Smirnov one-sample test: d=0.153, p>.20, and d= 0.162, p>.20) and were compared using a parametric two-sample t-test. Concerning RT no significant difference between R and NR conditions was revealed (mean ± SD = 635.1 ± 190.66 and 598.9 ± 167.015 respectively, t=1.214, df=21). On the contrary, accuracy was significantly lower in the R condition, as compared to the NR condition (92.4 ± 2.6% and 97.8 ± 1.25% respectively; t=5.232, p<.001, df=21).

Imaging data

Whole-head analysis - Rhyme detection task

In a first step of analysis, main effects for the rhyme detection task were investigated. Therefore, rhymed (R) and non-rhymed (NR) conditions were separately contrasted to the baseline (fixation cross and random button press). Table 1 and Figure 8 present regions that reveal significant supra-threshold BOLD-activation for each of the two experimental conditions, as compared with the empty trials. In both conditions a bilateral superior temporal fMRI pattern could be observed and exhibited a more expanded cluster of significant activation (p<0.05, FWE corrected) in the right, as compared to the left hemisphere. Notably, the peak activation in the right auditory-related cortex of the posterior temporal lobe was more anteriorially and medially situated in the R (44 -14 12), than in the NR condition (62 -16 -2).

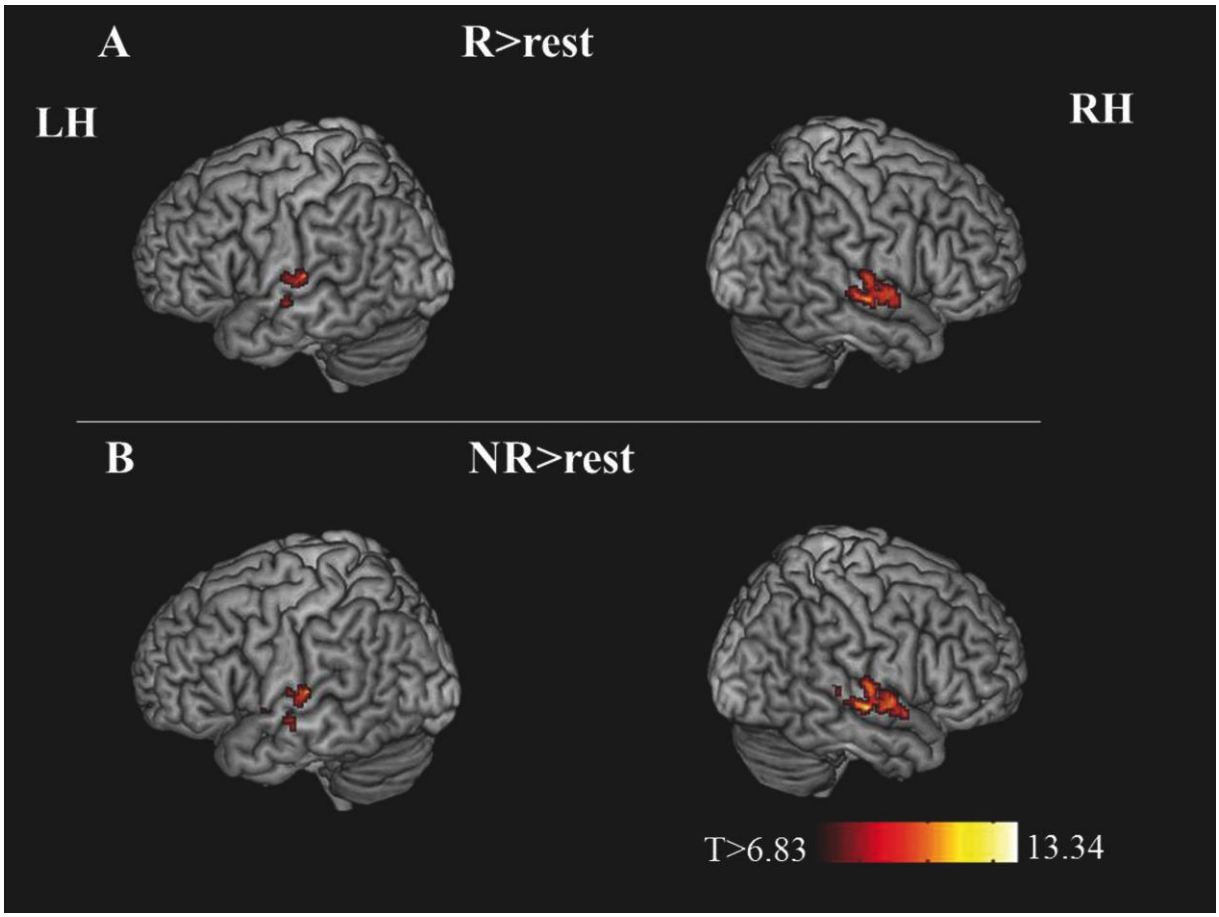

Figure 8. Brain areas showing significantly greater activation during the processing of A) rhymed and B) non-rhymed condition compared to rest. Each cluster is thresholded at $p<0.05$, FWE corrected with a spatial extent minimum of 20 contiguous voxels per cluster. The corresponding cortical regions, cluster sizes, peak T-values and MNI coordinates can be found in Table 1.

To statistically test for this rightward temporal lateralization in cluster size for both contrasts (R>rest, NR>rest) for each subject's statistic map (first-level contrast), left and right cluster sizes within the superior temporal gyrus were extracted and subjected to a paired sample t-test. As depicted in Figure 9, temporal cluster size was significantly larger in the right, than the left hemisphere in the R condition ($t=6.513$, $p<0.001$, $df=21$). This was also the case for the NR condition ($t=5.029$, $p<0.001$, $df=21$).

Table 1. Brain areas showing significant increases for rhymed and non-rhymed condition relative to baseline

	Left Hemisphere					Right hemisphere				
Condition/Region	*T score*	*Voxels*	*x*	*y*	*z*	*T score*	*Voxels*	*x*	*y*	*Z*
rhyme>rest										
Superior temporal gyrus						13.34	322	44	-14	2
	11.94	102	-50	-22	12					
	8.29	47	-48	-2	6					
Total amount of voxels		149					322			
non-rhyme>rest						12.82	349	62	-16	-2
Superior temporal gyrus	12.08	104	-50	-22	12					
	8.52	22	-48	-2	6					
	7.89	40	-52	-12	-4					
Total amount of voxels		166					349			

Note: x,y,z = MNI coordinates of local maxima. Voxels=number of voxels at p<0.05 after family-wise correction for multiple comparisons across the whole brain.

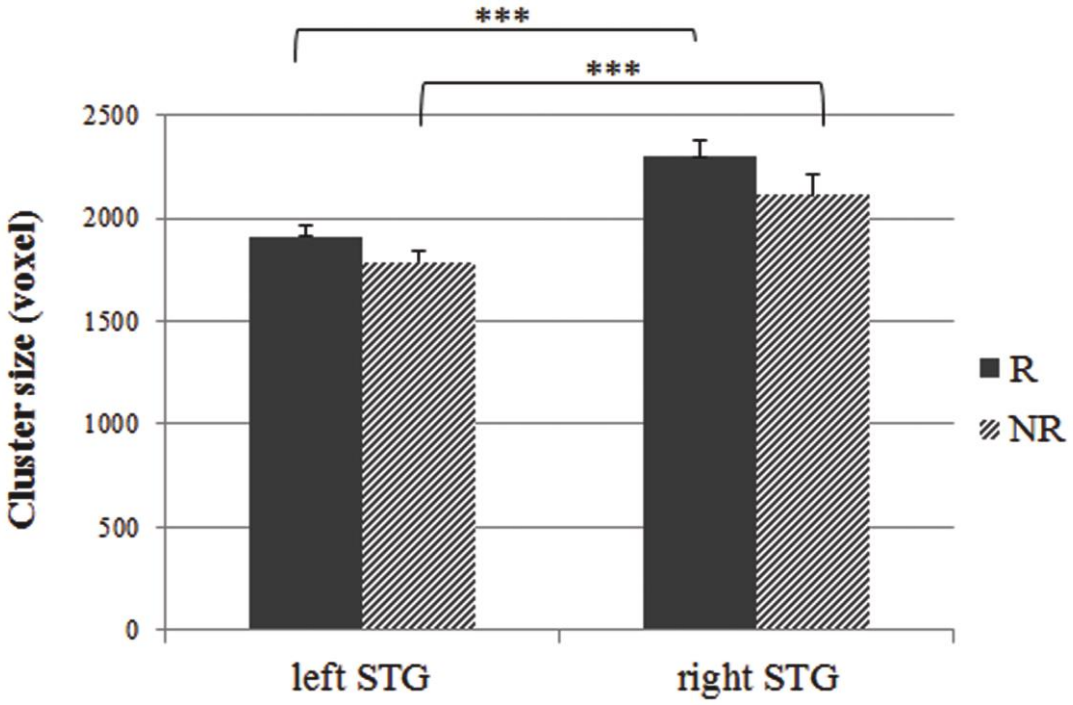

Figure 9. Size of activated clusters in bilateral superior temporal gyrus (STG). Mean value of each subjects' (n=22) cluster extent in R>rest and NR>rest contrasts (***p<0.001).

Rhymed vs. non-rhymed pseudo-sentences

The direct contrast between both conditions (Table 2, Figure 10) revealed increased BOLD-responses in the anterior insula and the deep opercular portion of the inferior frontal gyrus of the left hemisphere for rhymed, as compared with the non-rhymed pseudo-sentences ($p<0.05$ FWE corrected at cluster level, $k>25$). Since the expected effects in the direct contrasts are smaller than in the contrasts versus rest, we adopted the more liberal approach of clusterwise FWE correction, in order to not miss effects. The reverse contrast at the same threshold did not reveal any significantly different activation patterns between the NR and the R condition.

Table 2. Brain areas showing significant increases for rhymed compared to non-rhymed trials

Condition/Region	*H*	*T score*	*Voxels*	*x*	*y*	*z*
rhyme>non-rhyme						
Inferior frontal gyrus, opercular part	L	7.49	40	-52	14	0
anterior Insula	L	6.05	40	-28	24	6

Note: x,y,z = MNI coordinates of local maxima. H = hemisphere, L = left, Voxels = number of voxels. T scores and cluster size are reported if they are significant at $p<0.05$ after family-wise correction for multiple comparisons at cluster level ($k>25$)

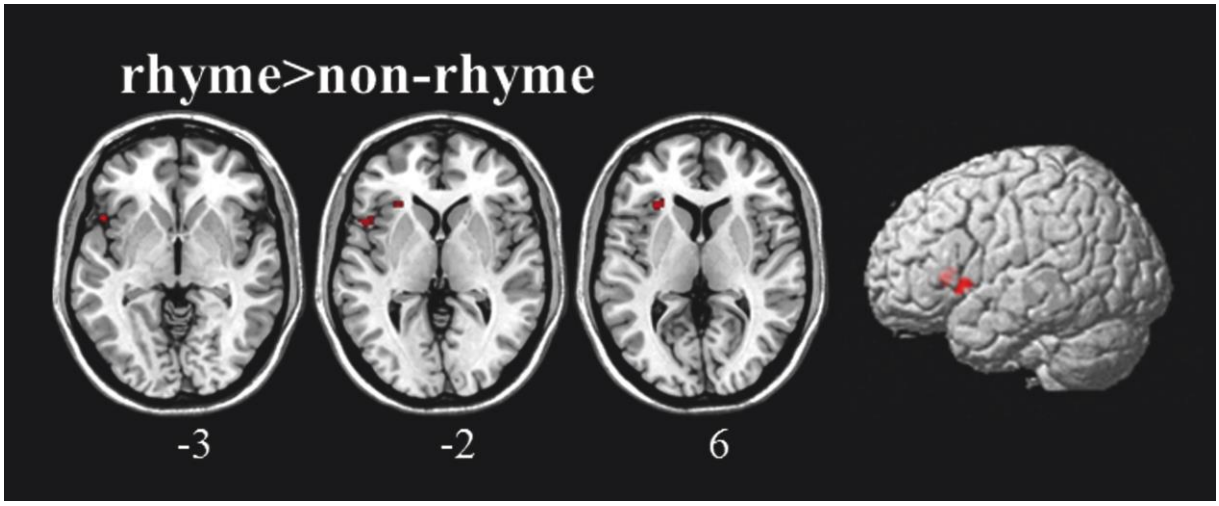

Figure 10. Brain areas showing significantly greater activation during the processing of rhymed compared to non-rhymed pseudo-sentences. Each cluster is thresholded at $p<0.05$, FWE-corrected at cluster level ($k>25$). The corresponding cortical regions, cluster sizes, peak T-values and MNI coordinates can be found in Table 2. Figures are displayed in neurological convention.

4.1.5 Discussion

In the current study, we investigated the neural basis of rhyme detection in healthy adults with a particular focus on lateralized processing.

At the behavioral level, we did not find a significant difference in reaction times between rhymed and non-rhymed conditions. This finding is consistent with studies using visually presented rhyming words (Khateb et al., 2000; Khateb et al., 2007; Rayman & Zaidel, 1991; Rugg & Barrett, 1987). The significantly increased error rate for rhymed as compared to non-rhymed sentences, was also evident in previous studies (Rayman & Zaidel, 1991; Rugg, 1984a; Rugg & Barrett, 1987). We assume that subjects showed a bias towards negative responses, when they were not completely sure of the answer. This may be due to the speed-demands placed upon them (caused by the instruction to "respond as quickly and accurately as possible") (Khateb et al., 2007).

The assumption that cortical fields in the right temporal lobe along the superior temporal gyrus and sulcus play an essential role in the analysis of the speech signal continues to receive ever-increasing support (Boemio, Fromm, Braun, & Poeppel, 2005; Hickok, 2001; Lattner, Meyer, & Friederici, 2005; Meyer et al., 2002, 2004; Vigneau et al., 2011). The right lateralized activation was observed while subjects were performing a rhyme detection task at the sentence level. This result buttresses the results of previous studies, which have investigated the auditory processing of slowly changing cues, namely, prosody and speech meter (Geiser et al., 2008; Meyer et al., 2002; Zhang et al., 2010). According to the "asymmetric sampling in time" hypothesis (AST), the auditory-related cortex of the right hemisphere is more inclined to process slowly changing acoustic cues (Meyer, 2008; Poeppel, 2003; Zatorre & Gandour, 2008). We posit that the right lateralized activation elicited during the explicit rhyme detection task complies with the predictions of this AST framework.

Akin to prosody and especially speech meter, rhymes serve as structural devices. Indeed, the segmentation of spoken sentences into single syllables is a suprasegmental computation, which relies on the analysis within larger time windows (~250ms). The fact that we found this lateralized activation in cluster-size irrespectively of the condition and task performance provides support to the hypothesis of a task-dependent, top-down modulation of lateralization effects in parts of the auditory-related cortex that may be preferentially sensitive to suprasegmental acoustic aspects speech and music (Brechmann & Scheich, 2005; Tervaniemi & Hugdahl, 2003). Geiser et al. (2008) found a similar right lateralization for speech rhythm

perception only in an explicit, task-driven processing condition, which implies that areas of the right (and left) STG are partly modulated by task demand (Poeppel et al., 1996).

The direct contrast between rhymed and non-rhymed trials demonstrated increased BOLD response in the left hemisphere for rhymed pseudo-sentences in the opercular part of the IFG and the anterior insula. The finding of increased rhyme related fronto-opercular activation is of specific interest, since rhyming targets should have been phonologically primed and would therefore require less processing than non-rhyming targets (Coch, Hart, & Mitra, 2008). However, a closer look at the literature pertaining to priming in auditory modality reveals a wide diversity of results. The best candidates for comparison to the present study are experiments that used sequentially presented primes and targets in the auditory modality. The most consistent findings in such studies are reduced activation for related targets in the bilateral IFG, as well as in the bilateral superior temporal gyrus (Orfanidou, Marslen-Wilson, & Davis, 2006; Vaden, Muftuler, & Hickok, 2010). Nonetheless, Orfanidou and colleagues (2006) only found priming effect for words and not for pseudowords. Notably, studies that did report priming effects in the IFG (Bergerbest, Ghahremani, & Gabrieli, 2004; Orfanidou, Marslen-Wilson, & Davis, 2006; Thiel et al., 2005) did not require explicit judgments between the prime and target word, as was the case in the present study.

To our knowledge, this is the first fMRI study that directly compares rhymed to non-rhymed pseudo-sentences. A small number of fMRI studies implementing an explicit rhyme detection task compared BOLD response associated with a rhyme detection task to other tasks. But the stimuli employed in these studies were visually presented (therefore involving grapho-phonemic conversion) and included words and/or pseudo words (e.g. Cousin et al., 2007), or single syllables (Sweet et al., 2008) thus, they obviously did not include direct contrasts between rhymed and non-rhymed sentences.

Therefore, we cannot rely upon these studies when attempting to elucidate the differences involved in auditory processing of rhymed versus non-rhymed items at the sentence-level.

Incidentally, various EEG investigations of the auditory modality have produced an electrophysiological rhyming effect for spoken word pairs. This effect is usually observed when a pair of words is presented and subjects are requested to make a phonemically based judgment and is typically expressed by a more negative bilateral posterior response for non-rhyming than for rhyming targets (Rugg, 1984b). Elsewhere, various researchers have demonstrated a reversal of this effect at lateral sites, that is, rhyming targets produced more negative responses than non-rhyming targets (Coch et al., 2005, 2011; Khateb et al., 2007). In

such an ERP study that included a rhyme-detection task with words, Coch et al. (2005) found a rhyming effect with a frontal leftward asymmetry in children and adults. They used a simple prime-target auditory rhyming paradigm with non-word stimuli (e.g. nin-rin, ked-voo). Interestingly, they found a more negative response to non-rhyming targets over posterior sites and an increased negativity to rhyming targets at lateral anterior sites. Subsequently, a visual rhyme-detection study conducted by Katheb et al. (2007) reported a specific left lateralized negativity for rhymed versus non-rhymed targets. Their estimated source localization indicated the major difference between rhyming and non-rhyming words as being positioned in predominantly left frontal and temporal areas. The fact that the rhyming effect can also be found when target words are spoken in a different voice than primes suggests that this effect is an index of phonological processing instead of a physical-acoustic mismatch (Praamstra & Stegeman, 1993). However, due to the inverse problem and the limited spatial resolution of the EEG technique, the informative value of EEG studies for the present work is quite limited and comparisons must be interpreted with caution.

In our study, we found a significant signal increase in the left frontal operculum and the left anterior insula during the rhymed trials as compared to the non-rhymed trials; this finding was absent during the reverse contrast (NR>R). The left inferior frontal gyrus (LIFG) has been shown to be related to a myriad of functions in speech processing (e.g. Davis et al., 2008; Lindenberg, Fangerau, & Seitz, 2007; Meyer & Jancke, 2006). Activation in the LIFG has been previously associated with segmentation processes or sublexical distinctions in different speech perception tasks (see Poeppel and Hickok, 2004) and a variety of syntactic and semantic operations (Hagoort, 2005; Ben Shalom & Poeppel, 2008). Nevertheless, there is currently no consensus with regards to the contribution that the LIFG makes to language processing (Friederici, 2011; Hickok, 2009). Besides unspecific, modality independent involvement in different language tasks, this region has been suggested to reflect aspects of articulatory rehearsal (Meyer et al., 2004) discrimination of subtle temporal acoustic cues during speech and non-speech (Zaehle, Geiser, Alter, Jancke, & Meyer, 2008), as well as auditory search (Giraud et al., 2004).

Previous studies were able to show that subvocal rehearsal processes are essentially mediated by parts of the LIFG (Paulesu et al., 1993). The posterior-dorsal aspect of the LIFG (corresponding to the opercular part) might be preferentially engaged in phonology-related, sublexical processes (Burton, Small, & Blumstein, 2000; Zurowski et al., 2002). This region is commonly suggested to be one part of the phonological loop in the Baddeley model (Paulesu, Frith, & Frackowiak, 1993; Smith & Jonides, 1999) and there is evidence that it

mediates phonological rehearsal. Hemodynamic changes in the opercular frontal inferior region have been previously associated with making phonological judgments (Démonet et al., 1992; Poldrack et al., 1999; Zatorre, Evans, Meyer, & Gjedde, 1992).

Since this study used pseudo-sentences, subjects could not build up expectations about the following words. Instead, they were required to maintain the critical segment from the first part of the sentence in their mind for three seconds until they heard the second critical segment, after which they made their decision by pressing a button box. Thus, it is clear that phonological rehearsal is needed, in order to detect rhyme; therefore, the involvement of inferior frontal regions is not surprising. The subjects in this study did not know whether the sentence that they were listening to rhymed or not until they heard the last syllable. Therefore, this result cannot be explained by working memory load *per se*; instead it is linked to the different outcomes resulting from the comparison between the syllables.

As suggested by Rogalsky and Hickok (2011), parts of the frontal operculum corresponding to regions in which we noted differences are essential for the integration of information that is maintained via articulatory rehearsal processes or decision-level processes, or both. The fact that we found activation in this region when we made a direct comparison between the rhymed versus the non-rhymed sentences bolsters the notion that the opercular portion of the LIFG plays a role in various decision-processes involved in a task that relies on phonological working memory. This interpretation also fits with results of previous studies, which found that the LIFG is involved in a adverse listening condition with enhanced demands on response selection (Binder, Liebenthal, Possing, Medler, & Ward, 2004; Giraud et al., 2004; Vaden et al., 2010; Zekveld, Heslenfeld, Festen, & Schoonhoven, 2006).

The direct comparison of rhymed with non-rhymed trials also revealed increased BOLD response in the left anterior insula. This region has previously been associated with diverse functions (Mutschler et al., 2009). Sharing extensive connections with different structures in temporal, frontal, and parietal cortices, the insula is perfectly situated for the task of integrating different sensory modalities. Previous research has identified the anterior insula as a key player in general processes of cognitive control (Cole & Schneider, 2007; Dosenbach et al., 2007). The anterior insula also seems to play a role in perception at each of the sensory modalities (Sterzer & Kleinschmidt, 2010). Besides its involvement in subvocal rehearsal processes during working memory activation, the left insula supports coordination processes in the complex articulatory programs that are needed during pseudoword processing (Ackermann & Riecker, 2004; Dronkers, Ogar, Willock, & Wilkins, 2004). Dyslectic children

show less activation than typically developing children in bilateral insulae during an auditory rhyme-detection task with words and pseudowords (Steinbrink, Ackermann, Lachmann, & Riecker, 2009). Furthermore, there is evidence that the left anterior insula is also involved in the phonological recognition of words (Bamiou, Musiek, & Luxon, 2003). Thus, our findings provide further evidence that the insula is involved in the auditory-motor network (Mutschler et al., 2009). However, our experimental design does not permit further discussion pertaining to the left anterior insula activation that we found.

The finding of significant differences in left frontal brain regions, which are associated with rhyme perception, coincides with results from the EEG studies discussed above. To reiterate, the aforementioned EEG studies produced significant differences for the direct contrasts between rhymed and non-rhymed stimuli. Due to the limited temporal resolution of fMRI technique, it is not possible to clearly link activation to a particular step of processing during the rhyme judgments. The stimuli used in both conditions did not contain syntactic or semantic information, and they did not differ in terms of intelligibility. Therefore, our finding that the reported left frontal brain activations were significant for the direct contrast level of analysis between rhymed and non-rhymed pseudo-sentences implies that these regions may not only be involved in articulatory rehearsal processes, but are also enmeshed in the last step of the analysis, namely, the detection of phonological matching.

Even though working memory load was theoretically identical in both conditions, we nevertheless, must consider that task difficulty may have contributed to the difference in brain activation between the conditions. It has previously been shown that activation of the LIFG can be modulated by task-difficulty (Zekveld et al., 2006). Since this is the first fMRI study that investigates auditory rhyme detection in an explicit paradigm at the sentence level, follow-up studies with more conditions that pose different cognitive demands should be introduced. Future research of this sort will prove helpful in disentangling brain responses that are associated with specific processes involved in auditory rhyme recognition.

4.1.6 Conclusion

We composed a rhyme detection task with pseudo-sentences to investigate the neural correlates of rhyme perception in healthy adults. Subjects in this study were requested to decide whether the last syllable of the pseudo-sentences rhymed or not. We found a task-related right-lateralized pattern of activation in the superior temporal lobe. This result implies that explicit rhyme processing at the sentence level – like prosody or meter in speech (Geiser et al., 2008; Meyer et al., 2002) – essentially relies on the processing in longer time windows wherefore the right temporal cortex has been proposed to be specialized (Poeppel, 2003). Direct comparisons between rhymed and non-rhymed pseudo-sentences showed increased activation for the correctly recognized rhymed trials in left fronto-opercular areas (deep frontal operculum and adjoining anterior insula). These regions have been previously linked to processes of phonological WM and articulatory rehearsal.

4.2 **Study II:** fMRI reveals lateralized pattern of brain activity modulated by the metrics of stimuli during sentence-level rhyme processing

Authors:

Martina A. Hurschler[1§],Franziskus Liem [2,3], Mathias S. Oechslin[3], Philipp Stämpfli[6,7], and Martin Meyer[1,3,4,5]

[1] Univ Zurich, Inst Psychol, Neuroplasticity and Learning in the Healthy Aging Brain (HAB LAB), CH-8050 Zurich, Switzerland
[2] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany
[3] International Normal Aging and Plasticity Imaging Center, University of Zurich, Switzerland
[4] University Research Priority Program "Dynamics of Healthy Aging", University of Zurich, Switzerland
[5] Cognitive Neuroscience, Institute of Psychology, University of Klagenfurt, Austria
[6] MR-Center of the Psychiatric University Hospital and the Department of Child and Adolescent Psychiatry, University of Zurich, Zurich, Switzerland
[7] Department of Psychiatry, Psychotherapy and Psychosomatics, Psychiatric Hospital, University of Zurich, Zurich, Switzerland

Published 2015 in: Brain and Language 147: 41-50.

Acknowledgements:

The authors acknowledge research support from the Swiss National Science Foundation (Grants 320030-120661 to MM), the ‘Fonds zur Forderung des akademischen Nachwuchses’ (FAN), and the University Research Program ‘Dynamics of Healthy Aging’ of the University of Zurich. We express our gratitude to James Perry for helpful comments on an earlier draft.

We are also thankful to Lutz Jäncke, Division of Neuropsychology, University of Zurich, for providing infrastructure and scanning resources necessary to perform the study.

4.2.1 Abstract

Our fMRI study investigates auditory rhyme processing in spoken language to further elucidate the topic of functional lateralization of language processing.

During scanning, 14 subjects listened to four different types of versed word strings and subsequently performed either a rhyme or a meter detection task. Our results show lateralization to auditory-related temporal regions in the right hemisphere irrespective of task. As for the left hemisphere we report responses in the supramarginal gyrus as well as in the opercular part of the inferior frontal gyrus modulated by the presence of regular meter and rhyme. The interaction of rhyme and meter was associated with increased involvement of the superior temporal sulcus and the putamen of the right hemisphere.

Overall, these findings support the notion of right-hemispheric specialization for suprasegmental analyses during processing of spoken sentences and provide neuroimaging evidence for the influence of metrics on auditory rhyme processing.

4.2.2 Introduction

„My words fly up, my thoughts remain below:

Words without thoughts never to heaven go.“

(William Shakespeare, Hamlet, Act 3 Scene 3)

Despite the fact that rhyme detection is believed to be one of the earliest developing and most simple phonological awareness skills and has been linked to the development of different language functions (Coch et al., 2005), there exists only parsimonious knowledge about the brain organization of rhyme in spoken language. By definition a rhyme is formed by the relationship between two phonological compounds in the way that rhyming word pairs are phonologically identical from the last accented vowel to the end of a word (e.g. “hat” and “cat”) (Bower & Bolton, 1969).

Rhyme, particularly when combined with a regular meter, is suggested to increase the saliency of a stimulus and thus to draw the listeners’ attention toward prosodic stimuli properties – in particular rhythm, stress and intonation (Obermeier et al., 2013). Like meter, rhyme represents a pattern of recurrence and is considered to serve as a kind of structure giving device. In that way rhyme as well as a regular rhythm both provide a degree of predictability, which supports memorization. In this context, several studies were able to demonstrate a beneficial effect of rhyme and meter on cognitive processing of the stimuli. For instance it could be shown that target words rhyming with a preceding word are easier to process (Coch et al., 2005; Kramer & Donchin, 1987; Rugg, 1984b) and that regular metrical structure is easier to remember than an irregular metrical pattern (Essens & Povel, 1985).

During the last years, the relevance of metric cues in different domains of language processing such as speech segmentation has been investigated by an increasing amount of studies. In particular, these studies were able to give evidence to the influence of metrical cues and predictions on syntactic (Schmidt-Kassow & Kotz, 2009), phonological (Cason & Schön, 2012) and semantic processing (Rothermich & Kotz, 2013).

Furthermore, meter and rhyme seem to have an impact on aesthetic liking and emotional involvement of the listener. In a recent behavioral study, Obermeier et al. (2013) were able to show that rhyme as well as regular meter both significantly contribute to the aesthetic and

emotional perception of poetry. Rhyming verses yielded more positive ratings than non-rhyming ones. Of pertinent interest in the context of the present study is also that the positive effect of rhyme was stronger in strophes with pseudowords.

The empirical investigation of rhyme processing is of interest from different perspectives. From a neurodevelopmental point of view, rhyme awareness is considered as one of the earliest developing forms of phonological awareness (Davids, van den Brink, van Turennout, & Verhoeven, 2011; Vloedgraven & Verhoeven, 2007). Behavioral studies were able to show not only that auditory rhyme detection skills develop early in life but also that rhyme awareness can serve as a predictor for later language skills such as learning to read (Avons et al., 1998; Bradley & Bryant, 1983; Goswami, 1993; Wood & Terrell, 1998). In line with this, dyslexic children and adults exhibited increased difficulties in rhyme detection tasks (Rumsey et al., 1992).

In order to be able to accurately detect rhyme on sentence-level, phonetic information needs to be memorized until the critical phoneme is encountered and the comparison with the previous item can be done. Rhyme judgments are therefore believed to engage the phonological store as well as a more active process of holding the information active through a subvocal rehearsal system (Baddeley et al., 1984; Baldo & Dronkers, 2006).

From the perspective of neuropsychological research, the investigation of auditory rhyme processing on the sentence level is - in our view - of specific interest pertaining to the question of functional lateralization in speech processing. The predominance of the left hemisphere in most aspects of speech and language processing is a well-evidenced fact in cognitive neuroscience (Friederici, 2012). Yet several facets of speech perception and the processing of spoken utterances have been associated with rightward lateralization in superior temporal regions: The right posterior superior temporal area has been found to be involved in processing speech prosody (Booth et al., 2002; Hesling, Dilharreguy, Clément, Bordessoules, & Allard, 2005; Meyer et al., 2002, Meyer et al., 2004; Zhang et al., 2010) vocal timbre (Lattner et al., 2005) as well as explicit processing of speech rhythm (Geiser et al., 2008) and meter (Hurschler, Liem, Jäncke, & Meyer, 2013).

However, a simple conception of prosody as a right-lateralized brain function *per se* does not do justice to the complexity of the topic. Instead increasing evidence in the field has led to different models of hemispheric processing of prosody based on functional or physical parameters (Van Lancker Sidtis, Pachana, Cummings, & Sidtis, 2006). While so-called functional models state that laterality is determined by the function of the prosodic stimulus

(such as linguistic vs affective), physical models link lateralized hemispheric processing to physical stimulus properties (e.g. temporal vs pitch elements.). It has been argued that these two approaches are not mutually exclusive but rather contribute in varying degrees to prosodic processes and thus are able to coexist (Van Lancker Sidtis et al., 2006).

These models make predictions of variable distinctness regarding the lateralization of brain responses in different speech perception tasks. One such prediction is based on the model of "asymmetric sampling in time" (Poeppel, 2003) and states that "phonemic phenomena occurring at the level of syllables should be more driven by right hemisphere mechanisms" (Poeppel, 2003, p. 25). Considering the fact that one of the most prominent characteristics of rhymes is the repetition of the same stressed vowels and thus rhyme detection essentially relies on such phonemic segmentation processes on syllable-level, the model predicts a task-related right-lateralized activation of the posterior superior temporal gyrus (pSTG) (Poeppel et al., 1996).

As highlighted by the conceptual framework by Van Lancker Siditis et al. (2006), speech mode and task essentially influence the pattern of brain regions involved in prosodic processing – in particular lateralization and involvement of basal ganglia.

So far, neural correlates of rhyme detection have almost exclusively been investigated on word level, often in visual modality and by means of electroencephalography (EEG) methods. Event-related potential (ERP) studies were able to show, that the brain shows different responses to rhyming and non-rhyming words (Rugg, 1984a; Rugg, 1984b; Wagensveld, Segers, van Alphen, Hagoort, & Verhoeven, 2012). This effect has typically been expressed by a more negative bilateral posterior response for nonrhyming targets (Rugg, 1984a) as well as a more negative response at lateral sites for rhyming targets (Coch et al., 2005; Khateb et al., 2000).

In a former fMRI study (Hurschler et al., 2013) we investigated the neural basis of auditory rhyme processing on the sentence level with word strings spoken in a metrical, verse-like manner. The rhyme detection task was associated with asymmetry in temporal cluster size with a more extended cluster in the right as compared to the left posterior superior temporal gyrus (STG) as well as stronger blood oxygen level dependent (BOLD) responses in the left frontal operculum and the anterior insula for the processing of rhymed as compared to non-rhymed versed word strings.

The aims of the present study are to extend prior knowledge about the neural correlates of auditory rhyme detection, and to gain specific insight in the interaction of the degree of

metrics and the presence of rhyme in auditory stimuli. In a broader sense, this study is meant to contribute to the topic of functional lateralization during speech perception, in particular in left and right perisylvian regions. The novelty of the present study thus particularly lies in the possibility to directly examine the influence of metricity on auditory rhyme processing.

The experimental conditions were constituted of four different types of versed word strings that systematically varied in the absence or presence of a rhyme and a regular meter. By using pseudowords we aim to rule out possible confounding effects of semantic expectation processes.

On one hand, this design allows us to investigate the neural network generally indicative of rhyme detection on sentence-level and thus to possibly replicate findings of our first explorative study. On the other hand, in addition to our first study, it also enables us to examine whether and how brain responses are mediated by metrical and rhythmical information available in spoken sentences. Based on the findings of our first study (Hurschler et al., 2013) as well as findings of the aforementioned studies and the prediction of the AST model (Poeppel, 2003) we hypothesize that the task (rhyme and meter detection) should recruit bilateral circuits in the auditory temporal regions with a clear functional lateralization to the right STG. We further expect that rhyme as well as meter detection recruit areas related to verbal working memory, such as, the left inferior parietal lobe and the left frontal operculum. Finally, assuming an interaction of rhyme and meter we expect activation in these regions to vary between conditions.

4.2.3 Methods

Subjects

Fourteen right-handed native Swissgerman speakers completed the fMRI study (21-33 years, mean age=25.3, 7 female). According to the Annett-Handedness Questionnaire (AHQ) (Annett, 1970) all participants were consistently right-handed (Handedness laterality quotient: M= 91.5, SD=8.8) and they reported no history of neurological, major medical, psychiatric, or hearing disorders. All subjects gave written consent in accordance with procedures approved by the local Ethics Committee and were paid for their participation.

Stimuli

A corpus of 160 versed word strings was recorded by a trained female speaker in a soundproof room. The stimuli resembled so-called "jabberwocky" pseudo sentences used in prior studies (Friederici, Meyer, & VonCramon, 2000; Hahne & Jescheniak, 2001). In contrast to typical jabberwocky sentences, the sentences applied in the current design do not contain systematic morphological markers, in order to minimize semantic and syntactic associations. All stimuli sentences were matched based on the amount of function words they contained.

The last syllable of the stimuli was either rhymed or not rhymed with the last syllable of the first part of the sentences and the sentences were either metrically consistent (=metrical) or not (=non-metrical). As "non-metrical" we define versed word strings that show irregularity in the stress pattern of the last part of the stimuli (three unaccented syllables in a row). By keeping the second part of the word string constant throughout all conditions and only changing the last pseudoword and/or the metricity of the last three syllables (according to the condition, see Figure 11) we focused participants' attention towards the end of each item.

As a result there exist four different types of versed word strings: metrical rhymed (MR), metrical non-rhymed (MNR), non-metrical rhymed (NMR) and non-metrical non-rhymed (NMNR) (see Figure 11). Each of the word strings exactly contained 12 syllables.

All stimulus items were analyzed by the means of PRAAT speech editor (Boersma, 2001) and normalized in amplitude to 70% of the loudest signal in a stimulus item and balanced with respect to mean intensity. The length of all stimuli was set to four seconds.

Stimuli were presented using Presentation software (Version 16.5, www.neurobs.com) and stimulus presentation was synchronized with the data acquisition by employing a 5 V TTL trigger pulse. A MR-compatible piezoelectric auditory stimulation system was used, that is incorporated into standard Philips headphones for binaural stimulus delivery.

"Sten **gein** un **sad** vom **Berz**, ber**lei**tis **meich** und **Lerz**" = **metrical rhymed (MR)**

"Sent **ka**hler **mehn** vom **Kars**, ber**lei**tis **meich** und **Foll**" = **metrical non-rhymed (MNR)**

"An**pri**se **del** vom **Seih**, ber**lei**tis meich und **Geih**" = **non-metrical rhymed (NMR)**

"Dor **gu**lan **Gert** vom **Surz**, ber**lei**tis meich und **Balcht**" = **non-metrical non-rhymed (NMNR)**

Figure 11. Examples of the four types of pseudo-sentences. Bold syllables were stressed.

Experimental Procedure

Subjects were familiarized with the task outside the scanner. They were instructed to answer as accurately and quickly as possible to a question (indicated by a visual cue) by button press after each auditory stimulus presentation. Each trial consisted of a pseudo-sentence, followed by a visual cue indicating the task, participants had to master. In half of the trials, they had to decide, whether or not the last sentence was rhymed ("R?") and in the other half of the sentences, whether or not the last sentence was metrical ("M?"). The two tasks were systematically balanced and randomized in order throughout all trials. This way, tasks were equally presented in all types of trials (MR, MNR, NMR, NMNR). Prior to scanning, all participants were given practice trials to familiarize with task procedures and the different types of items.

During scanning, the subjects indicated their response by pressing a button on the response box with either the index finger (=yes) or the middle finger (=no). Additionally, a total of twenty null events were created as additional baseline condition and were randomly included in the time course of the experiment. Subjects were instructed to press a random button in these trials (followed by "X?"). A fixation cross was presented for 500 milliseconds prior to each stimulus presentation. Stimuli were presented in a scanner-silent period (see Figure 12). The functional part of the scanning session lasted for 31.5 minutes.

Imaging Acquisition

In order to be able to present the stimuli in an interval devoid of auditory scanner noise, a clustered sparse temporal acquisition technique was used. This scheme combines the principles of a sparse temporal acquisition with a clustered acquisition (Liem et al., 2012; Schmidt et al., 2008; Zaehle et al., 2007). In each trial, three consecutive volumes were collected, in order to cover the peak of the event-related hemodynamic signal (See Figure 12).

Data were acquired at the Zurich University Hospital of Psychiatry, Switzerland.

Scanning was performed on a 3-T whole body MRI System (Philipps Achieva, Best, the Netherlands) equipped with an 8-channel head coil. Functional time series were collected from 16 transverse slices covering the entire perisylvian and extrasylvian cortex with a spatial resolution of 2.7 x 2.7 x 4 mm^3 by using a Sensitivity Encoded (SENSE) (Pruessmann et al., 1999) single-shot, gradient-echo planar sequence (acquisition matrix 80x80 Voxels, SENSE accelerator factor R=2, FOV= 220 mm, TE =35 ms). The volumes were acquired with an acquisition time of 1000 ms each, a flip angle = 68°, and a 7.5 s intercluster interval was employed; as a result, one trial lasted 10.5 seconds. Furthermore, a standard 3-D T1 weighted volume for anatomical reference was collected with a gradient echo sequence with a 0.94x0.94x1 mm spatial resolution (160 axial slices, acquisition matrix 256x256 voxels, FOV=240 x 240 mm, repetition time [TR] = 8.17 ms, flip angle=8°).

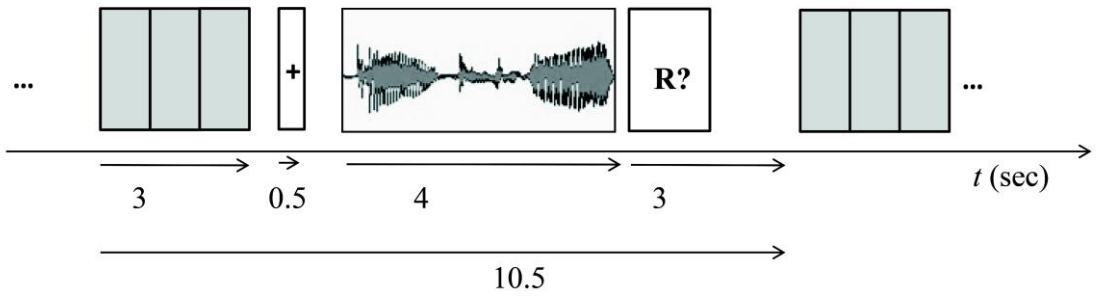

Figure 12. Clustered temporal acquisition scheme. Depicted are the three time points of acquisition and the stimulus presentation in one trial.

Data Analysis

Behavioral Data

Behavioral data analysis was performed by using SPSS Statistics 19.0 (SPSS inc.).

During the experiment in the scanner, behavioral performance data on the rhyme and meter detection task were collected. In a first step, subjects' individual reaction times (RT), as well as accuracy scores of the rhyme and meter detection task were compared using a repeated-measures t-test. In a second step, differences in accuracy rates and RT between the different types of sentences (independent of following task) were analyzed by applying 2x2 repeated-measures ANOVAs with the factors *rhyme* and *meter,* followed by repeated-measures t-tests (Bonferroni-corrected) in order to test for statistical differences between the measures in the different conditions. Greenhouse-Geisser correction was applied where sphericity assumption was violated (Geisser, 2003).

fMRI analysis

Pre-processing and statistical analysis of the neuroimaging data was performed by means of SPM8 (Wellcome Department of Imaging Neuroscience, Institute of Neurology, London, UK) in a Matlab (R2011b) environment (The MathWorks, MA).

In order to account for movement artifacts, all volumes were realigned to the first volume. Each subject's T1-weighted anatomical volume was coregistered to the mean images created by the realignment procedure. The subjects' T1-weighted images were normalized using the unified segmentation approach (Ashburner & Friston, 2005) and the resulting normalization matrix was applied to the functional volumes, transforming them into MNI space. Subsequently, functional images were smoothed using a Gaussian kernel with a 6mm full-width-at-half-maximum (FWHM) that increased the signal-to-noise ratio of the images. Due to the relatively little number of sampling points, a boxcar function (first order, window length = 3 seconds) was modeled for each trial. In addition, two regressors of no interest were included, in order to account for the T1-decay along the three volumes (Liem et al., 2012; Zaehle et al., 2007). The resulting contrast images from each of the first level fixed-effects analysis were entered into a full factorial second level design as well as one-sample t-tests (df=13).

Unless otherwise specified, results are reported at FWE- corrected level of $P<0.05$ (k=25).

Post-hoc region of interest analyses

In order to statistically test for lateralization in temporal involvement, two differential cluster analyses have been performed. First, cluster sizes of the contrast of all conditions against the baseline in the right and the left STG at the single-subject level ($p<0.001$, unc.) have been subjected to a 4x2 repeated measures ANOVA with the factors *condition* and *hemisphere*, followed by paired t-tests with the cluster extent in the right and the left STG for all conditions.

Secondly, in order to further investigate brain activation with respect to functional lateralization and condition-specific activation, statistical testing by means of spherical regions of interest (ROIs) was performed (Bosch, 2000). Therefore, three functional spherical ROIs in each hemisphere (STG, IFGop, SMG) were defined bilaterally based on mean group activation clusters. Center of the ROIs were the peak activation coordinates of the summed functional activation of all conditions within a 5 mm radius (see Table 3). For the ROIs in the SMG and the IFGop the center of left ROI was mirrored to the right hemisphere.

In a subsequent step, mean beta-values for each condition and participant were subjected to a repeated-measures ANOVA to analyze differences in brain activation in the ROIs across subjects between the different hemispheres and conditions.

For the bilateral ROIs in the STG, the SMG and the IFGop a repeated-measures 2x2x2 ANOVA with the factors *meter*, *rhyme*, and *hemisphere* were conducted.

The spherical ROIs were created by means of the MarsBar toolbox for SPM (http://marsbar.sourceforge.net/) (Brett et al., 2002). Via an in-house tool (based on Matlab environment) mean beta-values were extracted from first-level contrasts for each ROI and condition.

Table 3. Position of spherical ROIs

	Left hemisphere			Right hemisphere		
Region	X	y	z	x	y	z
STG	-56	-22	2	58	-8	-2
SMG	-46	-38	26	46	-38	26
IFGop	-52	6	8	52	6	8

Coordinates of center voxels of spherical ROIs (radius=5mm) are listed in MNI space.

STG=superior temporal gyrus; SMG=supramarginal gyrus; IFGop=opercular part of inferior frontal gyrus.

4.2.4 Results

Behavioral performance in the scanner

With respect to accuracy (percentage of correct answers per condition), no significant difference between rhyme (Rtask) and meter (Mtask) detection task was revealed (M=88.46, SD=4.23 and M=88.48, SD=13.02) respectively, T_{13}=-0.007, p=0.994). RT (in ms) was significantly shorter in the Rtask as compared to the Mtask (M=1099 ms, SD=225.95 and M=1233 ms, SD=215.10 respectively, T_{13}=-3.776, p=0.002, d_z=1.01). The high accuracy rates indicate that participants remained alert throughout the experiment and stayed on the task.

Concerning accuracy in the different type of sentences, we found a significant effect of *rhyme* ($F_{1,13}$=12.92, p=0.003, η_ρ^2=.50) and an interaction effect of *meter x rhyme* ($F_{1,13}$=7.89, p=0.15, η_ρ^2=.38). For RT, the ANOVA revealed a significant effect of *meter* ($F_{1,13}$=9.69, p=0.008, η_ρ^2=.43) and an interaction effect of *meter x rhyme* ($F_{1,13}$=8.6, p=0.012, η_ρ^2=.40).

Subsequent repeated measures t-tests showed that effects were due to higher accuracy and shorter RT in the MR condition as compared to the other conditions. However, only the difference in RT in MR and NMR and between accuracy between MR and MNR and MR and NMR was able to stand up to Bonferoni correction. No significant differences in either measure resulted between all other conditions.

Imaging data

Whole-brain analysis

In a first step of analysis, main effects for the different conditions and two types of task were investigated. A full factorial design with the factors *meter*, *rhyme*, and *task* revealed no significant task effects. Therefore, further analysis was performed pooled over the two behavioral tasks.

The average effect for all conditions as compared to the baseline trials yielded suprathreshold involvement of bilateral superior temporal gyri (STG), left supramarginal gyrus (SMG), the opercular part of the left inferior frontal gyrus (IFGop) and the right calcarine sulcus (see Figure 13a and Table 4).

In all conditions, cluster size in the STG is significantly larger in the right as compared to the left hemisphere. The repeated-measures ANOVA revealed main effects of *condition* ($F_{3,11}$=7.08, p=0.006, η_ρ^2=.659) and *hemisphere* ($F_{3,11}$=36.1, p<0.001, η_ρ^2=.735) and the post-hoc-t-tests yielded significant right lateralized effects for MR (T_{13}=6.14, p<0.001, d_z=1.6), MNR (T_{13}=7.2, p<0.001, d=1.93), NMR (T_{13}=3.5, p<0.004, d_z=0.93) and NMNR (T_{13}=6.3, p<0.001, d_z=1.7) condition against rest.

Interaction of rhyme and meter

The second level factorial design showed significantly increased BOLD responses for the interaction of rhyme and meter in the putamen and the posterior superior temporal sulcus (pSTS) of the right hemisphere (Table 4, Figure 13b).

Rhymed vs. non-rhymed metrical trials

The contrast MR vs. MNR (Table 5, Figure 13c) revealed two regions of the right hemisphere, which were significantly more strongly involved in metrical rhymed than in metrical non-rhymed sentences: the Rolandic operculum (ROP) and the hippocampus (HIP). The opposite contrast (MNR>MR) yielded no suprathreshold activation.

ROI analysis

Figure 14 indicates mean beta-values for the four experimental conditions in the functional ROIs (Bosch, 2000) whose positions are shown in Table 5. In all conditions, MR trials yielded strongest brain responses whereas NMR trials produced weakest activation.

A global (3x4x2) ANOVA with the within-factors *ROI*, *condition*, and *hemisphere* revealed main effects of *ROI* ($F_{2,12}$=14.74, p=0.001, η_ρ^2=.711), and *condition* ($F_{3,11}$=48.96, p<0.001, $\eta\rho^2$=.93), and an interaction effect between *ROI* x *hemisphere* ($F_{2,12}$=4.68, P<0.05, η_ρ^2=.48) indicating a different pattern of lateralization of brain responses in distinct regions of interest.

In a second step, for each ROI a separate 2x4 ANOVA with the factors *hemisphere* and *condition* was conducted (see Figure 4).

For the STG and the SMG the repeated-measures ANOVA only revealed a main effect *condition (*$F_{3,11}$=30.69, p<0.001, η_ρ^2=.893 and $F_{3,11}$=22.62, p<0.001, η_ρ^2=.68, respectively). This indicates that differences in brain activation are mainly modulated by the presence and/or absence of rhyme and regular meter in the word strings.

For the ROI in the opercular part of the IFG we found two main effects of *condition* ($F_{3,11}$=33.6, p<0.001, $\eta\rho^2$=.671) and *hemisphere* ($F_{1,13}$=5.7, p=0.033, η_ρ^2=.305), indicating lateralized brain activation in this region and modulation of activation by the condition (presence of meter and rhyme).

Table 4. Significant activation peaks provided by the full factorial group analysis

Condition/Region	*aal-Label*	*H*	*Z*	*Voxels*	*x*	*y*	*z*
Average effect of condition							
Superior temporal gyrus	T1	R	6.91	1673	58	-8	-2
Superior temporal gyrus	T1	L	6.27	856	-56	-22	2
Supramarginal gyrus	SMG	L	5.23	74	-46	-38	26
Inferior frontal gyrus, opercular part	F3OP	L	5.14	201	-52	6	8
Calcarine sulcus	V1	R	4.79	89	30	-62	12
Interaction meter x rhyme							
Putamen	PUT	R	5.14	39	24	4	12
Posterior superior temporal sulcus	T2	R	4.94	165	50	-56	12

Note: x,y,z = MNI coordinates of local maxima. H=hemisphere, L=left, R=right, Voxels=number of voxels. Z-scores and cluster size are reported if they are significant at p<0.05 after family-wise correction for multiple comparisons across the whole brain (k=25). Labeling corresponds to Tzourio-Mazoyer et al., 2002.

Table 5. Activation peaks provided by the contrast between the MR and the MNR condition.

Condition/Region	*aal-Label*	*H*	*T*	*Voxels*	*x*	*y*	*z*
MR>MNR							
Rolandic operculum	RO	R	7.96	85	44	-16	14
Hippocampus	HIP	R	7.24	23	32	-36	-2

Note: x,y,z = MNI coordinates of local maxima. H=hemisphere, L=left, R=right, Voxels=number of voxels. T-scores and cluster size are reported if they are significant at p<0.05 after family-wise correction for multiple comparisons at cluster level (k=20). Labeling corresponds to Tzourio-Mazoyer et al., 2002. MR=metrical rhymed, MNR=metrical non-rhymed.

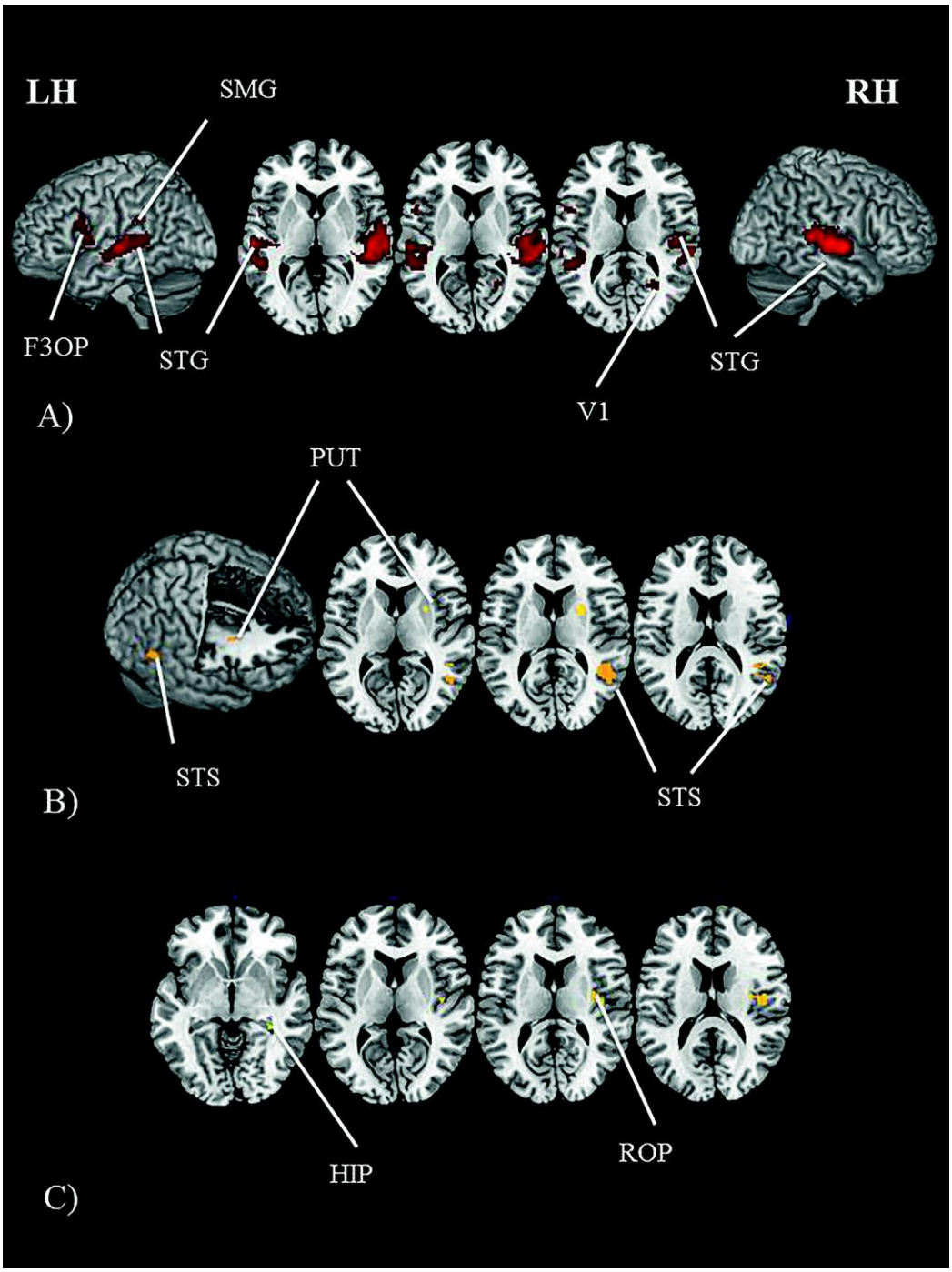

Figure 13. A) Main effect condition: Brain areas significantly modulated by the conditions. The corresponding cortical regions, cluster sizes, peak Z-scores and MNI coordinates can be found in Table 4.

B) Interaction meter x rhyme: Brain areas modulated by the interaction of meter and rhyme. Each cluster is thresholded at $p<0.05$, FWE-corrected with a spatial extent minimum of 20 contiguous voxels per cluster. The corresponding cortical regions, cluster sizes, peak Z-scores and MNI coordinates can be found in Table 4.

C) MR>MNR: Brain areas showing significantly greater activation during the processing of metrical rhymed (MR) as compared to metrical non-rhymed (MNR) trials. Each cluster is thresholded at $p<0.05$, FWE-corrected at cluster level with a spatial extent minimum of 20 contiguous voxels per cluster. The corresponding cortical regions, cluster sizes, peak T-scores and MNI coordinates can be found in Table 5.

Note: Figures are displayed in neurological convention. STG=superior temporal gyrus, STS=superior temporal sulcus, ROP=rolandic operculum, F3OP=opercular part of inferior frontal gyrus, HIP=Hippocampus, PUT=putamen, VI=calcarine suclus. SMG=supramarginal gyrus.

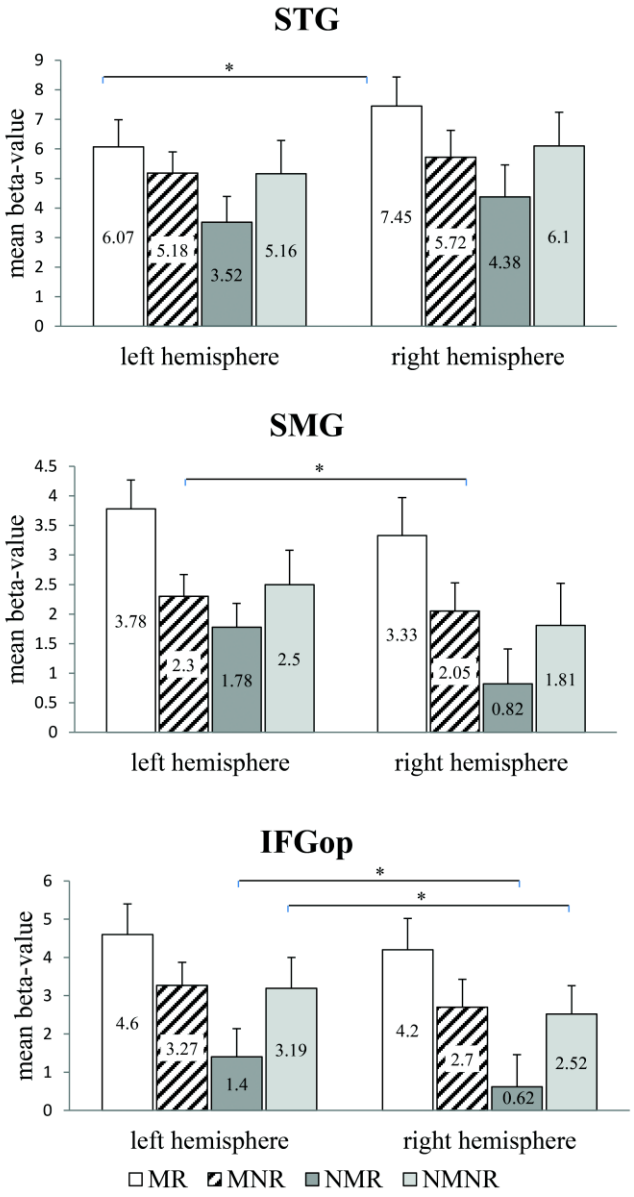

Figure 14. Condition-specific lateralization. Mean beta-values obtained from three bilateral regions of interest (ROIs). Error bars refer to the SEM (standard error of the mean). *p<0.05. Positions of ROIs are listed in Table 3.

Lateralization effects in ROIs

Post-hoc repeated measures t-tests in each ROI between activation in each condition and hemisphere revealed for the STG in the MR condition a significantly stronger activation in the right as compared to the left STG (T_{13}=-2.44, p=0.03, d_z=0.65.). In all other conditions, differences in activation between the ROIs in the two hemispheres did not reach significance

level. The difference between the MR and the MNR condition was only significant in the right STG (T_{13}=6.04, p<0.001, d_z=1.6).

In the SMG, activation in the left hemisphere was stronger in all conditions, but the difference between the hemispheres reached significance level only in the MNR condition (T_{13}=2.78, p=0.015, d=0.74). In the opercular part of the IFG, the stronger activation in the left as compared to the right hemisphere was significant in the NMR (T_{13}=2.9, p=0.012, d_z=0.77) and the NMNR (T_{13}=2.41, p=0.031, d_z=0.65) conditions.

Concerning the differences in activation between the conditions in all ROIs and in the two hemispheres, a similar pattern with significant differences between MR and NMR, MR and NMR as well as NMR and NMNR condition has been found. Remarkably, concerning the two non-rhymed conditions (MNR and NMNR) there were no significant differences in any of the ROIs.

4.2.5 Discussion

As expected, FMRI analyses revealed no significant differences in brain responses related to the rhyme and meter detection task – instead we observed differences associated with the different types of stimuli. Subjects did not know whether they had to fulfill the rhyme or meter task by the end of the stimuli. Thus they had to pay attention to both rhyme and meter while listening to the versed utterances. This leads us to the conclusion that the cognitive demand and thus probably the difficulty of task was mainly influenced by the presence and absence of rhyme and meter in the versed utterances.

Neural activation pattern underlying rhyme and meter detection

The finding of right-lateralized activation in bilateral superior temporal regions replicates the activation pattern reported in our previous fMRI study (Hurschler et al., 2013) and supports the widely agreed view that cortical fields in the right superior temporal lobe play an important role in processing suprasegmental cues available in speech signals. Furthermore, this result buttresses findings of previous studies investigating the processing of slowly changing auditory cues such as rhymes (Hurschler et al., 2013), sentence intonation (Meyer et al., 2002, 2004), linguistic prosody (Kreitewolf, Friederici, & Kriegstein, 2014), and speech meter (Geiser et al., 2008). In a recent fMRI study with parametrically manipulated speech stimuli, Liem et al. (2014) were able to show a shift in functional lateralization to the right

planum temporale (PT) and posterior lateral STG. The responses in the right posterior auditory-related cortex increase in strength the more suprasegmental acoustic modulation of the spoken utterances were obscured. These studies are also consistent with the ‘asymmetric sampling in time’ hypothesis (Poeppel, 2003) postulating that the auditory-related cortex of the right hemisphere is more adept at perceiving slowly changing acoustic cues.

Furthermore, the results of the whole-brain analysis show activation in the left SMG and the IFGop to be significantly modulated by both condition factors, namely rhyme and meter. The post-hoc ROI analyses of these regions shed light on the correlation of activation in the ROIs with the different rhyming conditions.

The left SMG has previously been suggested to be essential for sublexical acoustic-phonemic processing (Caplan, Gow, & Makris, 1995; Hickok & Poeppel, 2004; Kast, Bezzola, Jäncke, & Meyer, 2011; Paulesu et al., 1993) and to be substantially involved during conscious phonological decision making (Price, Moore, Humphreys, & Wise, 1997).. Further it has been identified to be involved in processes of phonological working memory, namely the temporary storage of verbal input (Jacquemot & Scott, 2006; Kreitewolf, Friederici, & Kriegstein, 2014; Obleser & Eisner, 2009).

Geiser et al. (2008) observed enhanced activation in the left SMG for isochronous (described as ‘exagerated’) as compared to nonisochronous (conversational) pseudo-sentences in an implicit processing condition. Our stimuli featured an isochronous meter, because they were all spoken in a verse-like manner. The assumption that the activation in the left SMG is somehow linked to the implicit processing of metrical aspects of the stimuli is supported by our finding of the ROI analysis that shows a significant lateralization to the left hemisphere only in the metrical non-rhymed (MNR) condition for the SMG of the IPL.

A similar pattern of activation in the different rhyming conditions showed up for the IFGop. The (left) IFG has previously been found to be activated in a variety of functions in speech processing (Davis et al., 2008; Lindenberg et al., 2007; Meyer & Jancke, 2006) and is commonly suggested to form an existential part of the phonological loop of working memory (Paulesu et al., 1993; Smith & Jonides, 1999). The region has specifically been suggested to be involved in articulatory rehearsal (Meyer et al., 2004; Rogalsky, Matchin, & Hickok, 2008) as well as phonological discrimination and phoneme-monitoring (Burton, Small, & Blumstein, 2000; Démonet et al., 1992; Démonet et al., 1994; Zatorre, Meyer, Gjedde, & Evans, 1996). These findings underpin the notion, that activation of the (left) IFGop is involved in phonetic judgments that require access to articulatory representations of the

stimuli and are predominantly found in active (as compared to passive listening) conditions (Zatorre et al., 1992; Zatorre et al., 1996). However, it should be mentioned that there is an ongoing debate about the language specificity of the different subparts of the frontal operculum. Recent multireceptor-based approaches demonstrate that the opercular and triangular part of the lateral and medial IFG in particular is by no means a homologous region (Amunts & Zilles, 2012). As reported by Amunts et al. (2010) different subparts of the IFG differ in their specific receptor expression patterns and thus also very probably in their signal processing properties. Such subdivisions of the opercular part of the IFG are also supported by results provided by various functional imaging studies. For example, activation in the ventral part of IFGop has been found to be related to syntactic processing (Friederici, 2006; Indefrey et al., 2001) whereas the dorsal IFGop showed to be involved in phonological processing (Heim & Friederici, 2003). At first glance our results are in line with this notion of an increased involvement of the dorsal IFGop in phonological processes.

However, we think that it is not really convenient to loosely and solely attribute complex cognitive functions to distinct brain regions by simply labeling it, for example, a 'rhyme-specific region'. Instead, during the recent past it has been proposed that distinct regions should be considered parts of large-scale networks with respect to both function and structure (Moran & Zaki, 2013). Very recently it has been proposed that (particularly the left) IFG does not perform any linguistic processing proper but instead that the role of inferior regions during language processing is to accomplish general aspects of cognitive control and conflict resolution (Bornkessel-Schlesewsky & Schlesewsky, 2013; Novick, Trueswell, & Thompson-Schill, 2005).

There is an increasing amount of models proposing the duality of ventral and dorsal processing streams to connect temporal, parietal and frontal regions during language processing (Bornkessel-Schlesewsky & Schlesewsky, 2013; Friederici, 2012; Hickok & Poeppel, 2004; Rauschecker, 1998; Rauschecker & Scott, 2009; Specht, 2014; Weiller, Bormann, Saur, Musso, & Rijntjes, 2011). According to the evidently well appreciated framework by Hickok & Poeppel (Hickok & Poeppel, 2004; Hickok & Poeppel, 2007) a ventral pathway, involving superior and middle portions of the left and right temporal lobes is supposed to subserve auditory-to-meaning mapping (speech recognition). A (left) dorsal stream, which involves structures in the frontal lobe, the posterior dorsal-most part of the temporal lobe and the inferior parietal lobe is stated to support auditory-to motor-mapping. In this context it has been suggested that sub-lexical phonological and verbal working memory tasks involve a virtually identical temporal-parietal-frontal network (Hickok & Poeppel, 2000;

Hickok & Poeppel, 2004) thus implying that such tasks rely on sensory-motor integration in the auditory dorsal stream.

Furthermore it has been proposed that the role of the dorsal stream should be considered in a more general domain-independent manner as the capacity to analyze the temporal or spectral sequence of segments (Belin & Zatorre, 2000; Rauschecker, 1998; Rauschecker & Scott, 2009). Our findings of increased activation in a network including bilateral STG, left SMG of IPL and left IFGop during attentively listening to versed word strings and fulfilling a rhyme as well as a meter detection task are in line with this notion.

The rhyme as well as the meter detection task revealed bilateral, right lateralized activation in the STG. In a recent fMRI study, Perrone-Bertolotti et al. (2013) found a comparable lateralized network to be activated during the auditory perception of prosodic focus when participants had to decide whether or not the sentences they heard contained contrastive focus (on the subject or the object) or not. The authors interpreted their finding of increased activation in temporal, parietal, and frontal regions during focused as compared to neutral condition in the context of the dual stream framework. While they attributed the right dominant STG activation to longer timescale computations and involvement of the ventral stream, the activation in the parietal and frontal regions was explained by an interplay between the two hemispheres in a auditory-motor hub and thus involvement of the dorsal stream (Perrone-Bertolotti et al., 2013).

Taken together, our results bolster the view that the left IFGop plays an important role in phonological detection processes that require phonological rehearsal (Meyer et al., 2004). The findings are in line with the general notion of a domain-independent dorsal stream in the frame of a dual route of speech processing that integrates elemental acoustic and cognitive functions. Eventually we discussed the dual stream models as we think that it is not appropriate to discuss the potential function of isolated cortical regions. We rather think that it is more justified and beneficial to discuss of findings in the context of networks that organize the interplay between several adjacent and remote regions that apparently contribute to the processing of the versed word strings.

Influence of metrics on rhyme processing

The finding of a strong interaction effect of rhyme and meter supports the notion that rhyme perception is modulated by regular metrics of the stimuli. Regular metrics draw the attention of the listener to a specific stimulus and thus enhance its saliency (Large & Jones, 1999; Obermeier et al., 2013). This notion finds support in our finding of enhanced accuracy and reduced reaction times in metrical rhymed sentences as compared to all other stimulus conditions.

The involvement of the right STS points to an important role this right-extrasylvian region plays for the processing of suprasegmental speech cues. Both the processing of rhyme and meter are supposed to rely on temporal analysis in a large-scale time window. This assumption finds support by a study about common substrates for the perception of intonation and speech rhythm that showed clear lateralization to right STS areas while subjects were passively listening to synthesized speech stimuli with varying rhythmic and intonational information (Zhang et al., 2010).

Of particular note is also the activation in the right putamen. The basal ganglia have previously been shown to be involved in processing suprasegmental speech cues, such as speech melody and rhythm perception (Geiser et al., 2008; Meyer et al., 2002; Van Lancker Sidtis et al., 2006). In studies investigating music perception, the presence of beat structure increases activation in the putamen (Grahn, 2009; Grahn & Brett, 2007). Moreover, this association to the putamen was confirmed even when rhythm of the stimuli was unrelated to the experimental task (Grahn & Rowe, 2013). Grahn and Rowe (2013) investigated different stages of beat perception and found the greatest activation of the putamen for a beat prediction (and not detection) condition. Interestingly they noticed that direct repetition of a rhythm at the same beat rate elicited significantly greater brain responses compared with the repetition of only beat rate with a different rhythmic pattern. The authors interpret this finding in a way that the “internal” aspect of the prediction is essential for inducing the putamen activity. In line with this, we found neural activity in the putamen associated with the positive interaction of rhyme and meter with strongest activation for the MR condition, corresponding to implicit predictions about correct/regular rhyme and metrics.

Rhyme-specific activity in the right hemisphere

Finally we were interested in the direct contrast between metrical rhymed (MR) and metrical non-rhymed (MNR) trials. For this comparison we found increased BOLD response in the right Rolandic operculum (ROP) and the right hippocampus (HIP). In our preceding fMRI study (Hurschler et al., 2013) we used a simple explicit rhyme detection task and found increased rhyme-related neural recruitment of the left anterior insula and the IFGop. Notably, due to the performed task we hypothesized, that this activation was linked to the last step of the rhyme judgment, namely, the detection of phonological matching. In the present design we placed our focus on different processes in rhyme detection that are supposed to occur in a more automatized manner and less linked to processes of expectancy. At the end of the sentence, participants did not yet know whether or not they had to fulfill the rhyme or the meter detection task. In that sense, the finding of increased activation of right Rolandic operculum (ROP) and right hippocampus (HIP) is more likely to be associated with the pure experience of resolved rhyme in metrical sentences.

The ROP of the right hemisphere has been found to support the processing of speech melody. Meyer et al. (2002) found increased activation of the right ROP for prosodic as compared to normal speech in an implicit task (detection of active vs passive voice) thus pointing to a higher susceptibility of the right auditory regions for processing slow pitch movements. This finding gets further support by a subsequent study (Meyer et al., 2004) demonstrating increased right ROP activation due to degraded speech (low-pass filtered speech stimuli containing only prosodic parameters while lacking lexical and syntactic information) as compared to normal speech stimuli. The authors propose that activation in the right ROP could be explained by sub-articulatory processes during silent rehearsal of the stimuli. This suggestion is corroborated by studies reporting the ROP to be involved in covert speech production (Wildgruber, Ackermann, Klose, Kardatzki, & Grodd, 1996) and covert speech processing inducing sub-articulation (Kiehl, Laurens, & Liddle, 2002). Our results additionally point to a relationship between right ROP and the outcome of such covert articulatory rehearsal strategies with enhanced brain responses to metrical rhymed sentences, which, proved by highest accuracy rates, represented the lowest task demands.

Concerning the activation in the right HIP, the comparisons with findings of a study investigating the emotional valence of word processing is probably interesting. Kuchinke et al. (2005) found increased activation in the right HIP associated with processing words with positive as compared to negative valence. Combining this result with the recent findings of

Obermeier et al. (2013) who propose that rhyming stimuli lead to more positively perceived and experienced emotions we could hypothesize that this hippocampal activation may substantiate a neural correlate of the positive appreciation of a perceived rhyme. However, due to the lack of comparable fMRI studies on the topic of rhyme processing on the sentence level this assumption has to be considered speculative.

4.2.6 Conclusion

Our data demonstrated lateralization in auditory-related regions of the right hemisphere in an active listening and target detection task, when participants pay attention to rhyme as well as metrics of the stimuli. In accordance with a previous study (Hurschler et al., 2013) our results suggest that processing rhymed words in spoken sentences essentially relies on a right temporal network that is supposed to subserve suprasegmental acoustic processing

Further we found increased activation in the left SMG of the left IPL and the left IFGop modulated by the presence of rhyme and regular meter. This circuit has previously been linked to phonological cache and phonological rehearsal respectively. Thus this finding evidences the involvement of cognitive processes tied to explicit rhyme and meter detection tasks.

Compared to non-rhymed trials, metrical rhymed trials were associated with increased activation of the ROP and the right hippocampus in the right hemisphere. The positive interaction effect of rhyme and meter we found in the right STS and the right putamen not only underscores the role of these areas in integrating suprasegmental cues in speech processing but also demonstrates the essential impact of metrics on rhyme processing.

5. GENERAL DISCUSSION

By means of clustered-sparse fMRI technique, the present thesis aimed to investigate the neural correlates of auditory rhyme processing and thus to provide further insight into the relationship between slowly changing acoustic modulations and right auditory-related cortex functions in general.

As findings of the single studies have been discussed in the discussion sections of the two original research articles, the following chapter will only briefly summarize the single results and interpretations. Subsequently, the most important findings will be integrated in the context of the research questions and aims stated earlier (see Chapter 3). Finally this part concludes with an elaboration on open questions and implications for further research on the topic.

The first study investigated the neural correlates of the performance of an explicit rhyme detection task with pseudo-sentences in healthy adults. This study provided a first insight into general neural circuits that form the basis of auditory rhyme detection at sentence-level. The task per se revealed brain responses in bilateral STG with a significant lateralization to the right hemisphere concerning cluster size of brain response. The data showed that successful detection of rhyming as compared to non-rhyming items is associated with activation in the left anterior insula and the opercular part of the left IFG. Our results thus suggest involvement of these regions in the last step of a rhyme detection task, namely the actual judgment of rhyme and the execution of the decision – and most probably also of the outcome of subjects' internal expectations about rhyme.

The second study was designed with a different task. This provided two additional insights as compared to the first study. On one hand, it allowed us to better control for expectations of rhyme and the possible confundation between rhyme detection and (implicit) expectancy effects. By introducing a second suprasegmental task (meter detection) and the fact that subjects had to answer the question about rhyme or meter *after* stimulus presentation (and thus did not know the task until the end of each trial), we were able to investigate brain responses we believe to be more specific to the experience of rhyme.

On the other hand, manipulating a second factor, namely metrics of the stimuli, enabled us to gain insight into neural correlations of interaction effects of rhyme and metrics. Our results on

one side replicated the finding of the first study, of a right-lateralized superior temporal network underlying rhyme detection on sentence-level, and on the other side underpin the role of the left IFG and left SMG in sentential rhyme detection. Furthermore we were able to show right lateralized activation in STS and the putamen associated with the interaction of meter and rhyme.

5.1 Neural processes involved in sentence-level rhyme processing

In our first research question, we asked for the neural correlates of auditory rhyme processing on sentence-level.

Research question 1:
What are the basic neural correlates of auditory rhyme processing at sentence-level?

Based on presumably involved processes we hypothesized to find (i) bilateral activation in auditory related cortices as well as (ii) involvement of regions linked to working memory, such as the SMG and the IFG.

In fact, rhyme detection in pseudo-sentences showed to be associated with a bilateral pattern of activation in the temporal auditory-related regions. Additionally, particularly with increased load of auditory working memory, by presenting the task at the end of the stimuli (see study II), data show enhanced involvement of the left IFGop and the left SMG. Accurate performance of the rhyme detection task requires keeping the phonological information active until the critical syllable is encountered. This process involves working memory. According to Baddeley's model (Baddeley, 1996; Baddeley, 2000) verbal memory is thought to be divided into a subvocal rehearsal system as well as a phonological store. While the phonological store is suggested to be able to store auditory/verbal information for a very short period of time, articulatory rehearsal is a more active process responsible for the maintenance of the information held in the phonological store (Baldo & Dronkers, 2006). Rhyme judgments have been supposed to engage both of these processes (Baddeley et al., 1984; Besner, 1987).

Several neuroimaging studies investigating working memory found activation in the left IFG (mostly in the opercular part, corresponding to BA 44) particularly related to articulatory

rehearsal (for an overview see Baddeley, 2003). Contrary to this, the left IPL (in particular the SMG) has been proposed to subserve the phonological store (e.g. Chein & Fiez, 2001; Henson, Burgess, & Frith, 2000; Paulesu et al., 1993).

Considering a possible connection between activations found in the STG, the IFG and the SMG during auditory rhyme judgments, our results can be interpreted in the framework of a "dual stream model" of speech processing. In analogy with the widely-accepted concept of a dorsal "where" and ventral "what" stream in the visual system (Mishkin & Ungerleider, 1982), an increasing amount of current models assume such a dual system for language processes to connect temporal and frontal cortices (Friederici, 2012; Hickok & Poeppel, 2004; Rauschecker, 1998; Scott et al., 2000; Weiller et al., 2011) (see also Chapter 2.2). Most of these models propose a ventral stream involved in mapping sound onto meaning, and a dorsal stream concerned with mapping sound onto articulatory based representations, respectively sensory motor integration processes (Hickok & Poeppel, 2000; Hickok & Poeppel, 2004; Weiller et al., 2011). Based on neuroimaging findings and the assumption that verbal working memory is a special case of auditory-motor integration, Hickok and Poeppel (2004) suggest that sub-lexical speech tasks rely on a dorsal stream network identical to that involved in verbal working memory tasks and thus to essentially involve the left IFG (particularly the opercular part), the left IPL and the left STG. Our findings of activation in these regions related to the performance of an auditory rhyme detection task with pseudo-sentences (thus ruling out semantic processes and increasing working memory demands as compared to tasks using words or syllables) are in line with this assumption. The fact that we found these regions equally involved in the rhyme-detection and the meter-detection task give further support to the recent notion, that activation in the dorsal stream is rather linked to the computational processes involved in the task than the linguistic properties of the speech stimuli itself. In a very recent elaboration of the dorsal-ventral-stream framework, Bornkessel-Schlesewsky and Schlesewsky (2013) propose that the dorsal stream engages in the time-dependent combination of elements and especially the frontal regions are concerned with general aspects of cognitive control rather than linguistic processing per se.

In both studies we directly contrasted metrical rhymed (MR) to metrical non-rhymed (MNR) trials and found increased neural responses to MR as compared to MNR pseudo-sentences. However, the locations of clusters of significant activation related to this comparison differ between the studies. While in Study I we found this rhyme-specific effect in the left anterior

insula and the opercular part of the left IFG, in Study II increased activation correlated to rhymed sentences was located in the rolandic operculum (ROP) and the hippocampus (HIP) of the right hemisphere

It seems plausible that differences in the experimental design account for these differences. Study I employed a very simple rhyme detection task on metrical pseudo-sentences. Differences between rhymed and non-rhymed trials thus can only be related to the different outcome of the decision process. Even though we used pseudo-sentences and subjects did not know whether or not they were presented with a rhymed item until the very last syllable, it cannot be excluded that they implicitly expected a rhyme and thus the response also reflects the occurrence of this expectation.

In study II, task demands were increased by (randomly) presenting one of two different tasks after the auditory presentation of the pseudo-sentences. Hence subjects had to pay attention to rhymes as well as metrics of the pseudo-sentences during the stimuli presentation. By introducing the task after stimulus presentation, such expectancy effects are minimized and the neural response (right HIP and right ROP) linked to the detection of rhymed as compared to non-rhymed stimuli is likely to be more closely related to the experience of rhyme per se. Particularly the activation in the right HIP might be interpreted in terms of emotional valence of stimuli (Kuchinke et al., 2005) and is in line with behavioral results showing rhyming stimuli to lead to more positive emotion ratings (Obermeier et al., 2013). However, in order to be able to disentangle different processes involved in rhyme processing, future studies need to employ very sophisticated designs varying not only cognitive demands of the tasks but also linguistic properties of the stimuli such as semantic content and including behavioral measures and ratings.

As stated in our second research question, we were further interested in the influence of metrics on the neural processes underlying rhyme detection.

Research question 2:
How are these processes of auditory rhyme detection influenced by the metrics of the stimuli?

As expected, metrics did have a significant modulating effect on rhyme processing. As reported in study II, we found the strongest response in all regions of interest (STS, left SMG,

left IFGop) in conditions where rhyme was accompanied by a regular meter. Furthermore, the interaction of rhyme and meter showed to be related to increased activation of two right-hemispheric regions, namely the putamen and the STS. Akin to rhyme, metrics are a structural device and increase the saliency of stimuli. Thus it seems likely that a regular meter enhances expectancy processes and thus modulates neural response at the time of resolution of rhyme detection (critical syllable). Moreover it has recently been shown that rhyme as well as meter enhance emotional appraisal of stimuli (Obermeier et al., 2013). Results of the second study point to an enhancing effect of metrics on the neural response underlying rhyme detection. However, future research is needed to investigate the specific effects of the presence of metrics on rhyme detection.

5.2 Functional lateralization during speech processing

The third research question addressed the issue of lateralization during a sentence-level rhyme detection task and hypothesized that – according to the predictions of the AST hypothesis – we should find a right lateralized pattern of activation in auditory related cortices.

Research question 3:

Does sentence-level rhyme detection lead to increased activation of right hemispheric auditory related regions?

Despite the fact that it has become widely accepted that also the right (non-dominant) hemisphere is involved in speech processing (Jung-Beeman, 2005), there is no clear consensus yet concerning the kind of its contribution. Our results provide further support to the notion that processing of slowly changing speech features, such as the segmentation into syllables, essentially relies on contributions of right hemispheric temporal regions. In both studies we were able to show a rightward lateralization in superior temporal regions associated with rhyme processing. This finding is in line with the predictions of the AST hypothesis (Poeppel, 2003), suggesting an increased activation of the right auditory-related cortex during processing of temporal analysis in longer time windows (such as segmentation into syllables as required for rhyme detection). This finding is in line with a recent study by Liem et al. (2013), reporting increased rightward lateralization corresponding to increased temporal integration windows in a pattern-matching task with sentences. Together, these

results give support to the notion, that the prediction of the AST framework also holds true in longer, more natural sounding stimuli.

5.3 Open questions and future directions

5.3.1 Rhyme detection in the context of language impairment

As repeatedly mentioned, in spite of the practical relevance of rhyme detection as a basic phonological awareness skill in the context of language development, there is hardly any basic knowledge concerning the neural correlates of this ability in the "healthy" brain.

The ability to recognize rhyme depends on the capacity to segment syllables into their constituents and to compare them (van Alphen et al., 2004), and this has been repeatedly stated to be a predictor of later reading comprehension skills (Bird, Bishop, & Freeman, 1995; Mody, Studdert-Kennedy, & Brady, 1997). Dyslectic as well as specific language impaired children show a marked delay in the development of the ability to detect rhyme (van Alphen et al., 2004). Moreover it was shown that children with specific language impairments (SLI) have problems remembering lines of nursery rhymes and tend to recall rhymes in an unconventional order (Fazio, 1997). Even though clinical implications are beyond the scope of this thesis, such findings emphasize the relevance of the topic and underpin the significance of gaining knowledge regarding neural circuits involved in successful rhyme detection.

In both of our studies we found task-specific involvement of areas previously linked to the working memory (more specifically the phonological loop), namely the opercular part of the IFG and the SMG of the left hemisphere. Interestingly, both of these regions have repeatedly been shown to display a significant lack of lateralization to the left hemisphere in dyslectics and language impaired individuals during phonological and other language tasks (Guibert et al., 2011). These findings are corroborated by behavioral studies showing poor performance in SLI subjects in verbal memory tasks (e.g. Archibald & Gathercole, 2007). It therefore seems to be an interesting approach to compare processes underlying auditory rhyme detection between healthy and SLI subjects.

5.3.2 Life-span perspective

In the past few years, effects of aging on speech perception have received increased scientific attention. In particular, it has been shown that older listeners tend to exhibit more difficulties particularly when speech is rapid or accompanied by noise (Fostick, Ben-Artzi, & Babkoff, 2013). Furthermore, older listeners showed impaired temporal resolution in gap detection and discrimination tasks independent of age-related hearing loss (e.g. Fitzgibbons & Gordon-Salant, 1994). In addition to effects on basic auditory processing, aging also has evidenced effects on cognitive abilities such as working memory, processing speed and executive functions (Tun, Williams, Small, & Hafter, 2012).

Moreover, aging seems to have an effect on functional lateralization during different cognitive tasks. In a very general and unspecified way, it has been proposed that age-related cognitive declines affect brain functions associated with the right hemisphere to a greater degree or alternatively, and that the right hemisphere shows greater age-related decline than the left hemisphere (Cabeza, 2002; Dolcos, Rice, & Cabeza, 2002).

In the context of the present thesis and on the basis of the findings briefly summarized here it would be very interesting to investigate age-related effects on neural correlates of rhyme detection as a measure of speech processing including different cognitive and phonological abilities. It would be a particularly important challenge to investigate the predictions of the AST hypothesis on age-related effects on lateralization in such a design, thus to bridge existing gaps between audiology and neurocognitive sciences, and also to contribute to a more holistic evaluation of the complexity of aging on speech processes (Tun et al., 2012).

5.3.3 Temporal resolution

As highlighted before, in the past, neural correlates of rhyme have been examined almost exclusively in EEG studies and at word level. Thirty years ago, Rugg (1984a) was the first to report a rhyme effect (with a peak around 450ms after target onset) in a visual rhyme judgment task with non-rhyming words eliciting a more negative deflection in the EEG waveform. Since then, various studies have examined the properties of this N450 effect and it could among others been shown, that the component can also be elicited by auditory stimuli and even when prime and target are spoken by different speakers (Praamstra & Stegeman, 1993). So far – to our knowledge – no studies have investigated this effect in a condition with auditory presented sentences (and/or pseudo-sentences). Contrary to fMRI measuring EEG and recording ERPs has the advantage of being able to provide insight into neural processes

taking place immediately after presentation of the stimuli. Combining the excellent temporal resolution of EEG method with the detailed knowledge about functional neuroanatomical correlates gained from functional neuroimaging, as reported in this thesis will provide much more precise insight into the time course of single processing steps during rhyme processing.

5.3.4 Influence of semantics

The empirical studies of this dissertation explicitly aimed to exclude influences of obvious semantic processes in order to be able to link observed brain activations with a high probability to rhyme processing per se.

This seems especially important, considering the brain regions that have been previously reported to be involved in semantic processing.

The IFG as well as the SMG in the left hemisphere have been shown to be involved in semantic priming (Copland, Zubicaray, McMahon, & Eastburn, 2007; Rossell, Price, & Nobre, 2003). In so-called “expectancy-based priming” subjects are suggested to develop expectancies of potential targets – this would definitely be the case by using real sentences. After the first part of the sentence, participants would expect a specific word to come at the end of the stimulus – thus the brain response recorded at the end of the stimulus would very likely be linked to arrival versus violation of this expectation.

However, to what extent pseudo-sentences still involve semantic processes is not easily answered. Future studies need to explicitly compare auditory rhyme processing with “normal” sentences, as compared to pseudo-sentences, in order to differentiate between semantic and sub-lexical processing.

6. REFERENCES

Abrams, D. A., Nicol, T., Zecker, S., & Kraus, N. (2008). Right-Hemisphere Auditory Cortex Is Dominant for Coding Syllable Patterns in Speech. *Journal of Neuroscience, 28*(15), 3958–3965.

Ackermann, H., & Riecker, A. (2004). The contribution of the insula to motor aspects of speech production: a review and a hypothesis. *Brain and Language, 89*(2), 320–328.

Amaro, E., Williams, Steve C R, Shergill, S. S., Fu, C., MacSweeney, M., Picchioni, M. M., Brammer, M.J., McGuire, P.K. (2002). Acoustic noise and functional magnetic resonance imaging: current strategies and future prospects. *Journal of Magnetic Resonance Imaging, 16*(5), 497–510.

Amunts, K., Lenzen, M., Friederici, A. D., Schleicher, A., Morosan, P., Palomero-Gallagher, N., & Zilles, K. (2010). Broca's region: novel organizational principles and multiple receptor mapping. *PLoS biology, 8*(9).

Amunts, K., & Zilles, K. (2012). Architecture and organizational principles of Broca's region. *Trends in Cognitive Sciences, 16*(8), 418–426.

Annett, M. (1970). A classification of hand preference by association analysis. *British Journal of Psychology, 61*(3), 303–321.

Archibald, L. M., & Gathercole, S. E. (2007). The complexities of complex memory span: Storage and processing deficits in specific language impairment. *Journal of Memory and Language, 57*(2), 177–194.

Ashburner, J., & Friston, K. J. (2005). Unified segmentation. *NeuroImage, 26(3),* 839–851.

Avons, S. E., Wragg, C. A., Cupples, L., & Lovegrove, W. J. (1998). Measures of phonological short-term memory and their relationship to vocabulary development. *Applied Psycholinguistics, 19*, 583–601.

Baddeley (2000). The episodic buffer: a new component of working memory? *Trends in Cognitive Sciences, 4*(11), 417–423.

Baddeley, A. (1996). The fractionation of working memory. *Proceedings of the National Academy of Sciences of the United States of America, 93*(24), 13468–13472.

Baddeley, A., Lewis, V., & Valler, G. (1984). Exploring the articulatory loop. *The Quarterly Journal of Experimental Psychology, 36*(2), 467–478.

Baddeley, A. (2003). Working memory: looking back and looking forward. *Nature reviews. Neuroscience, 4*(10), 829–839.

Baldo, J. V., & Dronkers, N. F. (2006). The role of inferior parietal and inferior frontal cortex in working memory. *Neuropsychology, 20*(5), 529–538.

Bamiou, D. E., Musiek, F. E., & Luxon, L. M. (2003). The insula (Island of Reil) and its role in auditory processing. Literature review. *Brain research reviews, 42*(2), 143–154.

Belin, P., & Zatorre, R. J. (2000). 'What', 'where' and 'how' in auditory cortex. *Nature neuroscience, 3*(10), 965–966.

Belin, P., Zilbovicius, M., Crozier, S., Thivard, L., Fontaine, A., Masure, M. C., & Samson, Y. (1998). Lateralization of speech and auditory temporal processing. *Journal of Cognitive Neuroscience, 10*(4), 536–540.

Ben Shalom, D., & Poeppel, D. (2008). Functional anatomic models of language: assembling the pieces. *The Neuroscientist, 14*(1), 119–127.

Bergerbest, D., Ghahremani, D., & Gabrieli, J. D. (2004). Neural correlates of auditory repetition priming: reduced fMRI activation in the auditory cortex. *Journal of Cognitive Neuroscience, 16*(6), 966–977.

Besner, D. (1987). Phonology, lexical access in reading, and articulatory suppression: a critical review. *The Quarterly Journal of Experimental Psychology Section A: Human Experimental Psychology, 39*(3), 467-478.

Binder, J. R., Frost, J. A., Hammeke, T. A., Cox, R. W., Rao, S. M., & Prieto, T. (1997). Human brain language areas identified by functional magnetic resonance imaging. *The Journal of Neuroscience, 17(*1), 353–362.

Binder, J. R., Frost, J. A., Hammeke, T. A., Rao, S. M., & Cox, R. W. (1996). Function of the left planum temporale in auditory and linguistic processing. *Brain, 119*, 1239–1247.

Binder, J. R., Liebenthal, E., Possing, E. T., Medler, D. A., & Ward, B. D. (2004). Neural correlates of sensory and decision processes in auditory object identification. *Nature neuroscience, 7*(3), 295–301.

Binkofski, F., & Buccino, G. (2004). Motor functions of the Broca's region. *Brain and Language, 89*(2), 362–369.

Bird, J., Bishop, D. V., & Freeman, N. H. (1995). Phonological awareness and literacy development in children with expressive phonological impairments. *Journal of Speech and Hearing Research, 38*(2), 446–462.

Boemio, A., Fromm, S., Braun, A., & Poeppel, D. (2005). Hierarchical and asymmetric temporal sensitivity in human auditory cortices. *Nature neuroscience, 8*(3), 389–395.

Boersma, P. (2001). Praat, a system for doing phonetics by computer. *Glot Int, 5*, 341–345.

Bogen, J. E., & Bogen, G. M. (1976). Wernicke's region--Where is it? *Annals of the New York Academy of Sciences, 280*, 834–843.

Bookheimer, S. (2002). Functional MRI of language: new approaches to understanding the cortical organization of semantic processing. *Annual Review of Neuroscience, 25*, 151–188.

Booth, J. R., Burman, D. D., Meyer, J. R., Gitelman, D. R., Parrish, T. B., & Mesulam, M. M. (2002). Functional anatomy of intra- and cross-modal lexical tasks. *NeuroImage, 16*(1), 7–22.

Booth, J. R., Burman, D. D., Meyer, J. R., Gitelman, D. R., Parrish, T. B., & Mesulam, M. M. (2004). Development of brain mechanisms for processing orthographic and phonologic representations. *Journal of Cognitive Neuroscience, 16*(7), 1234–1249.

Bornkessel-Schlesewsky, I., & Schlesewsky, M. (2013). Reconciling time, space and function: A new dorsal–ventral stream model of sentence comprehension. *Brain and Language, 125*(1), 60–76.

Bosch, V. (2000). Statistical analysis of multi-subject fMRI data: assessment of focal activations. *Journal of Magnetic Resonance Imaging, 11*(1), 61–64.

Bower, G. H., & Bolton, L. S. (1969). Why are rhymes easy to learn? *Journal of Experimental Psychology, 82*(3), 453-461.

Bradley, L., & Bryant, P. E. (1983). Categorizing sounds and learning to read: a causal connection. *Nature, 310*, 419-421.

Brechmann, A., & Scheich, H. (2005). Hemispheric shifts of sound representation in auditory cortex with conceptual listening. *Cerebral Cortex, 15*(5), 578–587.

Brett, M., Anton, J.-L., Valabregue, R., & Poline, J.-B. Region of interest analysis using an SPM toolbox [abstract] Presented at the 8th International Conference on Functional Mapping of the Human Brain, June 2-6, 2002, Sendai, Japan. Available on CD-ROM in *NeuroImage*, 16.

Broca, P. (1861). Remarques sur le siège de la faculté du language articulé; suivies d'une observation d'aphémie (perte de la parole). *Bulletins de la Société d'Anthropologie, 36*, 330–357.

Brunswick, N., McCrory, E., Price, C. J., Frith, C. D., & Frith, U. (1999). Explicit and implicit processing of words and pseudowords by adult developmental dyslexics: A search for Wernicke's Wortschatz? *Brain, 122*, 1901–1917.

Bryant, P. E., Bradley, L., MacLean, M., & Crossland, J. (1989). Nursery rhymes, phonological skills and reading. *Journal of Child Language, 16*(2), 407–428.

Bryant, P. E., MacLean, M., Bradley, L. L., & Crossland, J. (1990). Rhyme and alliteration, phoneme detection, and learning to read. *Developmental Psychology, 26*(3), 429–438.

Burton, M. W., Small, S. L., & Blumstein, S. E. (2000). The role of segmentation in phonological processing: an fMRI investigation. *Journal of Cognitive Neuroscience, 12*(4), 679–690.

Burton, M. W., Locasto, P. C., Krebs-Noble, D., & Gullapalli, R. P. (2005). A systematic investigation of the functional neuroanatomy of auditory and visual phonological processing. *NeuroImage, 26*(3), 647–661.

Cabeza, R. (2002). Hemsipheric asymmetry reduction in old adults: the HAROLD Model. *Psychol Aging 2002, 17*(1), 85–100.

Caplan, D., Gow, D., & Makris, N. (1995). Analysis of lesions by MRI in stroke patients with acoustic-phonetic processing deficits. *Neurology, 45*(2), 293–298.

Cardoso-Martins, C. (1994). Rhyme perception: global or analytical? *Journal of Experimental Child Psychology, 57*(1), 26–41.

Cason, N., & Schön, D. (2012). Rhythmic priming enhances the phonological processing of speech. *Neuropsychologia, 50*(11), 2652–2658.

Chein, J. M., & Fiez, J. A. (2001). Dissociation of verbal working memory system components using a delayed serial recall task. *Cerebral Cortex 11*(11), 1003–1014.

Coch, D., Grossi, G., Skendzel, W., & Neville, H. (2005). ERP nonword rhyming effects in children and adults. *Journal of Cognitive Neuroscience, 17*(1), 168–182.

Coch, D., Hart, T., & Mitra, P. (2008). Three kinds of rhymes: An ERP study. *Brain and Language, 104*(3), 230–243.

Coch, D., Mitra, P., George, E., & Berger, N. (2011). Letters rhyme: electrophysiological evidence from children and adults. *Developmental Neuropsychology, 36*(3), 302–318.

Cole, M. W., & Schneider, W. (2007). The cognitive control network: Integrated cortical regions with dissociable functions. *NeuroImage, 37*(1), 343–360.

Copland, D. A., Zubicaray, G. I., McMahon, K., & Eastburn, M. (2007). Neural correlates of semantic priming for ambiguous words: An event-related fMRI study. *Brain Research, 1131(1),* 163–172.

Cousin, E., Peyrin, C., Pichat, C., Lamalle, L., Le Bas, J.-F., & Baciu, M. (2007). Functional MRI approach for assessing hemispheric predominance of regions activated by a phonological and a semantic task. *European Journal of Radiology, 63*(2), 274–285.

Crosson, B., Rao, S. M., Woodley, S. J., Rosen, A. C., Bobholz, J. A., Mayer, A., Cunningham, J. M., Hammeke, T. A., Fuller S. A., Binder J. R., Cox, R. W., & Stein, E. A. (1999). Mapping of semantic, phonological, and orthographic verbal working memory in

normal adults with functional magnetic resonance imaging. *Neuropsychology*, 13(2), 171–187.

Davids, N., van den Brink, D., van Turennout, M., & Verhoeven, L. (2011). Task-related influences on neurophysiological assessment of auditory rhyme: implications for clinical studies. *Clinical Neurophysiology*, *122*(8), 1629–1636.

Davis, C., Kleinman, J. T., Newhart, M., Gingis, L., Pawlak, M., & Hillis, A. E. (2008). Speech and language functions that require a functioning Broca's area. *Brain and éanguage, 105*(1), 50–58.

Decety, J., Grèzes, J., Costes, N., Perani, D., Jeannerod, M., Procyk, E., et al. (1997). Brain activity during observation of actions. Influence of action content and subject's strategy. *Brain, 120*, 1763–1777.

Démonet, J. F., Chollet, F., Ramsay, S., Cardebat, D., Nespoulous, J. L., Wise, R., Rascol, A., & Frackowiak, R. (1992). The anatomy of phonological and semantic processing in normal subjects. *Brain, 115*, 1753–1768.

Démonet, J. F., Price, C., Wise, R., & Frackowiak, R. S. (1994). A PET study of cognitive strategies in normal subjects during language tasks. Influence of phonetic ambiguity and sequence processing on phoneme monitoring. *Brain, 117*, 671–682.

Devlin, J. T., Raley, J., Tunbridge, E., Lanary, K., Floyer-Lea, A., Narain, C., Cohen, I., Behrens, T., Jezzard, P., Matthews, P. M., & Moore, D. R. (2003). Functional asymmetry for auditory processing in human primary auditory cortex. *The Journal of Neuroscience, 23*(37), 11516–11522.

Di Salle, F., Formisano, E., Seifritz, E., Linden, D. E., Scheffler, K., Saulino, C., Tedeschi, G., Zanella, F.E., Pepino, A., Goebel, R., & Marciano, E. (2001). Functional fields in human auditory cortex revealed by time-resolved fMRI without interference of EPI noise. *NeuroImage, 13*(2), 328–338.

Dolcos, F., Rice, H. J., & Cabeza, R. (2002). Hemispheric asymmetry and aging: right hemisphere decline or asymmetry reduction. *Neuroscience & Biobehavioral Reviews 26*(7), 819–825.

Dosenbach, N. U., Fair, D., Miezin, F., Cohen, A. L., Wenger, K., Dosenbach, R. A., Fox, M. D., Snyder, A. Z., Vincent, J. L., Raichle, M. E., Schlaggar, B. L.,& Petersen, S. E. (2007). Distinct brain networks for adaptive and stable task control in humans. *Proceedings of the National Academy of Sciences of the United States of America, 104*(26), 11073–11078.

Dronkers, N., Ogar, J., Willock, S., & Wilkins, D. P. (2004). Confirming the role of the insula in coordinating complex but not simple articulatory movements. *Brain and Language, 91*(1), 23–24.

Dumay, N., Benraiss, A., Barriol, B., Colin, C., Radeau, M., & Besson, M. (2001). Behavioral and electrophysiological study of phonological priming between bisyllabic spoken words. *Journal of Cognitive Neuroscience, 13*(1), 121–143.

Eden, G., Joseph, J., Brown, H., Brown, C., & Zeffiro, T. (1999). Utilizing hemodynamic delay and dispersion to detect fMRI signal change without auditory interference: the behavior interleaved gradients technique. *Magnetic Resonance in Medicine, 41*(1), 13–20.

Efron, R. (1963). Temporal perception, Aphasia and déja vu. *Brain, 86*, 403–424.

Eling, P. (2011). Lichtheim's golden shot. *Cortex*, 47(4), 501-8

Essens, P. J., & Povel, D. J. (1985). Metrical and nonmetrical representations of temporal patterns. *Perception & Psychophysics*, *37*(1), 1–7.

Fazio, B. B. (1997). Learning a new poem: memory for connected speech and phonological awareness in low-income children with and without specific language impairment. *Journal of Speech, Language, and Hearing Research*, *40*(6), 1285–1297.

Fiez, J. A., Balota, D. A., Raichle, M. E., & Petersen, S. (1999). Effects of lexicality, frequency, and spelling-to-sound consistency on the functinal anatomy of reading. *Neuron, 24*, 205–218.

Fitzgibbons, P. J., & Gordon-Salant, S. (1994). Age effects on measures of auditory duration discrimination. *Journal of Speech, Language and Hearing Research, 37*(3), 662–670.

Fostick, L., Ben-Artzi, E., & Babkoff, H. (2013). Aging and speech perception: beyond hearing threshold and cognitive ability. *Journal of Basic and Clinical Physiology and Pharmacology, 2*4(3), 175–183.

Friederici, A. D. (2011). The brain basis of language processing: from structure to function. *Physiological Reviews, 91*(4), 1357–1392.

Friederici, A., Meyer, M., & von Cramon, D. (2000). Auditory language comprehension: an event-related fMRI study on the processing of syntactic and lexical information. *Brain and Language, 74*(2), 289–300.

Friederici, A. D. (2002). Towards a neural basis of auditory sentence processing. *Trends in Cognitive Sciences, 6*(2), 78–84.

Friederici, A. D. (2006). Broca's area and the ventral premotor cortex in language: functional differentiation and specificity. *Cortex, 42*(4), 472–475.

Friederici, A. D. (2012). The cortical language circuit: from auditory perception to sentence comprehension. *Trends in Cognitive Sciences, 16*(5), 262–268.

Friederici, A. D., Bahlmann, J., Heim, S., Schubotz, R. I., & Anwander, A. (2006). The brain differentiates human and non-human grammars: functional localization and structural connectivity. *Proceedings of the National Academy of Sciences of the United States of America, 103*(7), 2458–2463.

Friston, K. J., Zarahn, E., Josephs, O., Henson, R. N., & Dale, A. M. (1999). Stochastic designs in event-related fMRI. *NeuroImage, 10*(5), 607–619.

Gaab, N., Gabrieli, J. D., & Glover, G. (2007). Assessing the influence of scanner background noise on auditory processing. An fMRI study comparing auditory processing in the absence and presence of recorded scanner noise using a sparse design. *Human Brain Mapping, 28*(8), 721–732.

Gandour, J., Tong, Y., Wong, D., Talavage, T., Dzemidzic, M., Xu, Y., Li, X, & Lowe, M. (2004). Hemispheric roles in the perception of speech prosody. *NeuroImage, 23*(1), 344–357.

Geiser, E., Zaehle, T., Jancke, L., & Meyer, M. (2008). The neural correlate of speech rhythm as evidenced by metrical speech processing. *Journal of Cognitive Neuroscience, 20*(3), 541–552.

Geisser, S. (2003). The analysis of profile data--revisited. *Statistics in Medicine*, 22(21), 3337–3346.

Geschwind, N. (1965). Disconnexion syndromes in animals and man. *Brain, 88*(2), 237–294.

Gillon, G. (2004). Phonological awareness: from research to practice. New York: Guilford Press.

Giraud, A. L., Kell, C., Thierfelder, C., Sterzer, P., Russ, M. O., Preibisch, C., & Kleinschmidt, A. (2004). Contributions of sensory input, auditory search and verbal comprehension to cortical activity during speech processing. *Cerebral Cortex, 14*(3), 247–255.

Goswami, U. (1993). Phonological skills and learning to read. *Annals of the New York Academy of Sciences, 682*, 296–311.

Grahn, J. A., & Rowe, J. B. (2013). Finding and feeling the musical beat: striatal dissociations between detection and prediction of regularity. *Cerebral Cortex, 23(*4), 913–921.

Grahn, J. A. (2009). The role of the basal ganglia in beat perception: neuroimaging and neuropsychological investigations. *Annals of the New York Academy of Sciences, 1169*, 35–45.

Grahn, J. A., & Brett, M. (2007). Rhythm and beat perception in motor areas of the brain. *Journal of Cognitive Neuroscience, 19*(5), 893–906.

Greenberg, S. (1998). A syllable-centric framework for the evolution of spoken language. *Brain and Behavioral Sciences, 21*, 267–268.

Griffiths, T. D., Johnsrude, I., Dean, J. L., & Green, G. G. (1999). A common neural substrate for the analysis of pitch and duration pattern in segmented sound? *Neuroreport, 10*(18), 3825–3830.

Griffiths, T. D., & Warren, J. D. (2002). The planum temporale as a computational hub. *Trends in Neurosciences, 25*(7), 348–353.

Grodzinsky, Y. (2006). The language faculty, Broca's region, and the mirror system. *Cortex, 42(*4), 464–468.

Grodzinsky, Y., & Friederici, A. D. (2006). Neuroimaging of syntax and syntactic processing. *Current Opinion in Neurobiology, 16*(2), 240–246.

de Guibert, C., Maumet, C., Jannin, P., Ferré, J.-C., Tréguier, C., Barillot, C., Le Rumeur, E., Allaire, C., & Biraben A. (2011). Abnormal functional lateralization and activity of language brain areas in typical specific language impairment (developmental dysphasia). *Brain, 134*, 3044–3058.

Hagoort, P. (2005). On Broca, brain, and binding: a new framework. *Trends in Cognitive Sciences, 9*(9), 416–423.

Hahne, A., & Jescheniak, J. D. (2001). What's left if the Jabberwock gets the semantics? An ERP investigation into semantic and syntactic processes during auditory sentence comprehension. *Cognitive Brain Research, 11*(2), 199–212.

Hall, D. A., Haggard, M. P., Akeroyd, M. A., Palmer, A. R., Summerfield, A. Q., Elliott, M. R., Gurney, E. M., & Bowtell, R. W. (1999). "Sparse" temporal sampling in auditory fMRI. *Human Brain Mapping, 7*(3), 213–223.

Hamzei, F., Rijntjes, M., Dettmers, C., Glauche, V., Weiller, C., & Büchel, C. (2003). The human action recognition system and its relationship to Broca's area: an fMRI study. *NeuroImage, 19*(3), 637–644.

Heim, S., & Friederici, A. D. (2003). Phonological processing in language production: time course of brain activity. *Neuroreport, 14*(16), 2031–2033.

Henson, R. N., Burgess, N., & Frith, C. D. (2000). Recoding, storage, rehearsal and grouping in verbal short-term memory: an fMRI study. *Neuropsychologia, 38*(4), 426–440.

Herbster, A. N., Mintun, M. A., Nebes, R. D., & Becker, J. T. (1997). Regional cerebral blood flow during word and nonword reading. *Human Brain Mapping, 5*(2), 84–92.

Hernandez, N., Andersson, F., Edjlali, M., Hommet, C., Cottier, J. P., Destrieux, C., & Bonnet-Brilhault, F. (2013). Cerebral functional asymmetry and phonological performance in dyslexic adults. *Psychophysiology, 50*(12), 1226–1238.

Hesling, I., Clément, S., Bordessoules, M., & Allard, M. (2005). Cerebral mechanisms of prosodic integration: evidence from connected speech. *NeuroImage, 24*(4), 937–947.

Hesling, I., Dilharreguy, B., Clément, S., Bordessoules, M., & Allard, M. (2005). Cerebral mechanisms of prosodic sensory integration using low-frequency bands of connected speech. *Human Brain Mapping, 26*(3), 157–169.

Hickok, & Poeppel (2000). Towards a functional neuroanatomy of speech perception. *Trends in Cognitive Sciences, 4(*4), 131–138.

Hickok, G. (2001). Functional anatomy of speech perception and speech production: psycholinguistic implications. *Journal of Psycholinguistic Research, 30*(3), 225–235.

Hickok, G. (2009). The functional neuroanatomy of language. *Physics of Life Reviews, 6*(3), 121–143.

Hickok, G., & Poeppel, D. (2004). Dorsal and ventral streams: a framework for understanding aspects of the functional anatomy of language. *Cognition, 92*(1-2), 67–99.

Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature reviews. Neuroscience,* 8(5), 393–402.

Hoien, T., Lundberg, L., Stanovich, K. E., & Biaalid, I. K. (1995). Components of phonological awareness. *Reading and Writing, 7*, 171–188.

Humphries, C., Love, T., Swinney, D., & Hickok, G. (2005). Response of anterior temporal cortex to syntactic and prosodic manipulations during sentence processing. *Human Brain Mapping, 26*(2), 128–138.

Humphries, C., Willard, K., Buchsbaum, B., & Hickok, G. (2001). Role of anterior temporal cortex in auditory sentence comprehension: An fMRI study. *Neuroreport, 12*(8), 1749–1752.

Humphries, C., Binder, J. R., Medler, D. A., & Liebenthal, E. (2006). Syntactic and semantic modulation of neural activity during auditory sentence comprehension. *Journal of Cognitive Neuroscience, 18*(4), 665–679.

Hurschler, M. A., Liem, F., Jäncke, L., & Meyer, M. (2013). Right and left perisylvian cortex and left inferior frontal cortex mediate sentence-level rhyme detection in spoken language as revealed by sparse fMRI. *Human Brain Mapping, 34*(12), 3182–3192.

Indefrey, P., Brown, C. M., Hellwig, F., Amunts, K., Herzog, H., Seitz, R. J., & Hagoort, P. (2001). A neural correlate of syntactic encoding during speech production. *Proceedings of the National Academy of Sciences of the United States of America, 98*(10), 5933–5936.

Ischebeck, A., Friederici, A., & Alter, K. (2008). Processing prosodic boundaries in natural and hummed speech: an fMRI study. *Cerebral Cortex, 18*(3), 541–552.

Jacquemot, C., & Scott, S. K. (2006). What is the relationship between phonological short-term memory and speech processing? *Trends in Cognitive Sciences, 10*(11), 480–486.

Jamison, H. L., Watkins, K. E., Bishop, Dorothy V M, & Matthews, P. M. (2006). Hemispheric specialization for processing auditory nonspeech stimuli. *Cerebral Cortex, 16*(9), 1266–1275.

Jäncke, L. (2005). Methoden der Bildgebung in der Psychologie und den kognitiven Neurowissenschaften. Stuttgart: Kohlhammer.

Jäncke, L., Wüstenberg, T., Scheich, H., & Heinze, H.-J. (2002). Phonetic perception and the temporal cortex. *NeuroImage, 15*(4), 733–746.

Jung-Beeman, M. (2005). Bilateral brain processes for comprehending natural language. *Trends in Cognitive Sciences, 9*(11), 512–518.

Kareken, D. A., Lowe, M., Chen, S. H., Lurito, J., & Mathews, V. (2000). Word rhyming as a probe of hemispheric language dominance with functional magnetic resonance imaging. *Neuropsychiatry, Neuropsychology, and Behavioral Neurology, 13*(4), 264–270.

Kast, M., Bezzola, L., Jäncke, L., & Meyer, M. (2011). Multi- and unisensory decoding of words and nonwords result in differential brain responses in dyslexic and nondyslexic adults. *Brain and Language, 119*(3), 136–148.

Khateb, A., Pegna, A. J., Michel, C. M., Custodi, M. C., Landis, T., & Annoni, J. M. (2000). Semantic category and rhyming processing in the left and right cerebral hemisphere. *Laterality, 5*(1), 35–53.

Khateb, A., Pegna, A. J., Landis, T., Michel, C. M., Brunet, D., Seghier, M. L., & Annoni, J.-M. (2007). Rhyme processing in the brain: an ERP mapping study. *International Journal of Psychophysiology, 63*(3), 240–250.

Kiehl, K. A., Laurens, K. R., & Liddle, P. F. (2002). Reading anomalous sentences: an event-related fMRI study of semantic processing. *NeuroImage, 17*(2), 842–850.

Kotz, S. A., & Schwartze, M. (2010). Cortical speech processing unplugged: a timely subcortico-cortical framework. *Trends in Cognitive Sciences, 14*(9), 392–399.

Kovelman, I., Norton, E. S., Christodoulou, J. A., Gaab, N., Lieberman, D. A., Triantafyllou, C., Wolf, M., Whitfield-Gabrieli, S., & Gabrieli, J. D. (2012). Brain basis of phonological awareness for spoken language in children and its disruption in dyslexia. *Cerebral Cortex, 22*(4), 754–764.

Kramer, A. F., & Donchin, E. (1987). Brain potentials as indices of orthographic and phonological interaction during word matching. *Journal of Experimental Psychology. Learning, Memory, and Cognition, 13*(1), 76–86.

Kreitewolf, J., Friederici, A. D., & Kriegstein, K. von (2014). Hemispheric lateralization of linguistic prosody recognition in comparison to speech and speaker recognition. *NeuroImage, 102*, 332–344.

Kuchinke, L., Jacobs, A. M., Grubich, C., Võ, M. L.-H., Conrad, M., & Herrmann, M. (2005). Incidental effects of emotional valence in single word processing: An fMRI study. *NeuroImage, 28*(4), 1022–1032.

Kuest, J., & Karbe, H. (2002). Cortical activation studies in aphasia. *Current Neurology and Neuroscience Reports, 2(*6), 511–515.

Large, E. W., & Jones, M. R. (1999). The dynamics of attending: How people track time-varying events. *Psychological Review, 106*(1), 119–159.

Lattner, S., Meyer, M. E., & Friederici, A. D. (2005). Voice perception: Sex, pitch, and the right hemisphere. *Human Brain Mapping, 24*(1), 11–20.

Lichtheim, L. (1885). On aphasia. *Brain 7*, 433–84

Liégeois-Chauvel, C., de Graaf, J B, Laguitton, V., & Chauvel, P. (1999). Specialization of left auditory cortex for speech perception in man depends on temporal coding. *Cerebral Cortex 9*(5), 484–496.

Liem, F., Hurschler, M. A., Jancke, L., & Meyer, M. (2014). On the planum temporale lateralization in suprasegmental speech perception: Evidence from a study investigating behavior, structure, and function. *Human Brain Mapping, 35*(4), 1779–1789.

Liem, F., Lutz, K., Luechinger, R., Jäncke, L., & Meyer, M. (2012). Reducing the interval between volume acquisitions improves "sparse" scanning protocols in event-related auditory fMRI. *Brain Topography, 25*(2), 182–193.

Lindenberg, R., Fangerau, H., & Seitz, R. J. (2007). "Broca's area" as a collective term? *Brain and Language, 102*(1), 22–29.

Logothetis, N. K. (2003). The underpinnings of the BOLD functional magnetic resonance imaging signal. *The Journal of Neuroscience, 23*(10), 3963–3971.

Logothetis, N. K. (2008). What we can do and what we cannot do with fMRI. *Nature, 453*(7197), 869–878.

Logothetis, N. K., Pauls, J., Augath, M., Trinath, T., & Oeltermann, A. (2001). Neurophysiological investigation of the basis of the fMRI signal. *Nature, 412*(6843), 150–157.

Maess, B., Koelsch, S., Gunter, T. C., & Friederici, A. D. (2001). Musical syntax is processed in Broca's area: an MEG study. *Nature Neuroscience, 4*(5), 540–545.

Mazoyer, B. M., Tzourio, N., Frak, V., Syrota, A., Murayama, N., Levrier, O., et al. (1993). The cortical representation of speech. *Journal of Cognitive Neuroscience, 5*(4), 467–479.

McGettigan, C., & Scott, S. K. (2012). Cortical asymmetries in speech perception: what's wrong, what's right and what's left? *Trends in Cognitive Sciences*, 16(5), 269–276.

Meinschaefer, J., Hausmann, M., & Güntürkün, O. (1999). Laterality effects in the processing of syllable structure. *Brain and Language, 70*(2), 287–293.

Meyer, M. (2008). Functions of the left and right posterior temporal lobes during segmental and suprasegmental speech perception. *Zeitschrift für Neuropsychologie, 19*(2), 101–115.

Meyer, M., & Jancke, L. (2006). Involvement of the left and right frontal operculum in speech and nonspeech perception and production. In Y. Grodzinsky & K. Amunts (Eds.), Broca's Region. Involvement of the left and right frontal operculum in speech and nonspeech perception and production. New York: Oxford University Press.

Meyer, M., Alter, K., Friederici, A. D., Lohmann, G., & von Cramon, Y. D. (2002). fMRI reveals brain regions mediating slow prosodic modulations in spoken sentences. *Human Brain Mapping, 17*(2), 73–88.

Meyer, M., Steinhauer, K., Alter, K., Friederici, A. D., & von Cramon, Y. D. (2004). Brain activity varies with modulation of dynamic pitch variance in sentence melody. *Brain and Language, 89*(2), 277–289.

Meynert, T. (1866). Ein Fall von Sprachstörung, automatisch begründet. Redigiert von C. Braun, A. Duchek, L. Schlager. *Medizinische Jahrbücher*, *22*, 152–189.

Mishkin, M., & Ungerleider, L. G. (1982). Contribution of striate inputs to the visuospatial functions of parieto-preoccipital cortex in monkeys. *Behavioural Brain Research*, 6(1), 57–77.

Mody, M., Studdert-Kennedy, M., & Brady, S. (1997). Speech perception deficits in poor readers: auditory processing or phonological coding? *Journal of Experimental Child Psychology, 64*, 64(2), 199–231.

Moelker, A., & Pattynama, P. (2003). Acoustic noise concerns in functional magnetic resonance imaging. *Human Brain Mapping*, *20*(3), 123–141.

Moran, J. M., & Zaki, J. (2013). Functional neuroimaging and psychology: what have you done for me lately? *Journal of Cognitive Neuroscience*, *25*(6), 834–842.

Mutschler, I., Wieckhorst, B., Kowalevski, S., Derix, J., Wentlandt, J., Schulze-Bonhage, A., & Ball, T. (2009). Functional organization of the human anterior insular cortex. *Neuroscience Letters, 457*(2), 66–70.

Narain, C., Scott, S. K., Wise, Richard J S, Rosen, S., Leff, A., Iversen, S. D., & Matthews, P. M. (2003). Defining a left-lateralized response specific to intelligible speech using fMRI. *Cerebral Cortex, 13*(12), 1362–1368.

Noesselt, T., Shah, N. J., & Jäncke, L. (2003). Top-down and bottom-up modulation of language related areas--an fMRI study. *BMC Neuroscience, 4*(13).

Novick, J. M., Trueswell, J. C., & Thompson-Schill, S. L. (2005). Cognitive control and parsing: reexamining the role of Broca's area in sentence comprehension. Cognitive, Affective & Behavioral Neuroscience, 5(3), 263–281.

Obermeier, C., Menninghaus, W., Koppenfels, M. von, Raettig, T., Schmidt-Kassow, M., Otterbein, S., & Kotz, S. A. (2013). Aesthetic and emotional effects of meter and rhyme in poetry. *Frontiers in Psychology, 4*, 10.

Obleser, J., & Eisner, F. (2009). Pre-lexical abstraction of speech in the auditory cortex. *Trends in Cognitive Sciences*, *13*(1), 14–19.

Ogawa, S., Lee, T. M., Kay, A. R., & Tank, D. W. (1990). Brain magnetic resonance imaging with contrast dependent on blood oxygenation. *Proceedings of the National Academy of Sciences of the United States of America, 87*(24), 9868–9872.

Ogawa, S., Menon, R. S., Tank, D. W., Kim, S. G., Merkle, H., Ellermann, J. M., & Ugurbil, K. (1993). Functional brain mapping by blood oxygenation level-dependent contrast magnetic resonance imaging. A comparison of signal characteristics with a biophysical model. *Biophysical Journal, 64*(3), 803–812.

Orfanidou, E., Marslen-Wilson, W. D., & Davis, M. H. (2006). Neural response suppression predicts repetition priming of spoken words and pseudowords. *Journal of Cognitive Neuroscience, 18*(8), 1237–1252.

Paulesu, E., Frith, C. D., & Frackowiak, R. S. (1993). The neural correlates of the verbal component of working memory. *Nature, 362*(6418), 342–345.

Perrin, F., & García-Larrea, L. (2003). Modulation of the N400 potential during auditory phonological/semantic interaction. Brain research. *Cognitive Brain Research, 17*(1), 36–47.

Perrone-Bertolotti, M., Dohen, M., Lœvenbruck, H., Sato, M., Pichat, C., & Baciu, M. (2013). Neural correlates of the perception of contrastive prosodic focus in French: a functional magnetic resonance imaging study. *Human Brain Mapping*, *34*(10), 2574–2591.

Plante, E., Creusere, M., & Sabin, C. (2002). Dissociating sentential prosody from sentence processing: activation interacts with task demands. *NeuroImage, 17*(1), 401–410.

Poeppel, D., Yellin, E., Phillips, C., Roberts, T. P., Rowley, H. A., Wexler, K., & Marantz, A. (1996). Task-induced asymmetry of the auditory evoked M100 neuromagnetic field elicited by speech sounds. *Cognitive Brain Research, 4*(4), 231–242.

Poeppel, D. (2001). Pure word deafness and the bilateral processing of the speech code. *Cognitive Science, 25*, 679–693.

Poeppel, D. (2003). The analysis of speech in different temporal integration windows: cerebral lateralization as 'asymmetric sampling in time'. *Speech and Communication, 41*, 245–255.

Poeppel, D. (2012). The maps problem and the mapping problem: two challenges for a cognitive neuroscience of speech and language. *Cognitive Neuropsychology, 29*(1-2), 34–55.

Poeppel, D., Emmorey, K., Hickok, G., & Pylkkänen, L. (2012). Towards a new neurobiology of language. *The Journal of Neuroscience, 32*(41), 14125–14131.

Poeppel, D., & Hickok, G. (2004). Towards a new functional anatomy of language. *Cognition, 92*(1-2), 1–12.

Poldrack, R. A., Wagner, A. D., Prull, M. W., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. (1999). Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *NeuroImage, 10*(1), 15–35.

Praamstra, P., Meyer, A. S., & Levelt, W. J. (1994). Neurophysiological manifestations of phonological processing: Latency variation of a negative ERP component timelocked to phonological mismatch. *Journal of Cognitive Neuroscience, 6*(3), 204–219.

Praamstra, P., & Stegeman, D. F. (1993). Phonological effects on the auditory N400 event-related brain potential. Brain research. *Cognitive Brain Research,* 1(2), 73–86.

Price, C. (2000). The anatomy of language: Contributions from functional neuroimaging. *Journal of Anatomy, 197*, 335–359.

Price, C. J., Moore, C. J., Humphreys, G. W., & Wise, R. J. (1997). Segregating semantic from phonological processes during reading. *Journal of Cognitive Neuroscience, 9*(6), 727–733.

Price, C. J. (2012). A review and synthesis of the first 20 years of PET and fMRI studies of heard speech, spoken language and reading. *NeuroImage, 62*(2), 816–847.

Pruessmann, K. P., Weiger, M., Scheidegger, M. B., & Boesiger, P. (1999). SENSE: sensitivity encoding for fast MRI. *Magnetic Resonance in Medicine, 42*(5), 952–962.

Pugh, K. R., Shaywitz, B. A., Shaywitz, S. E., Constable, R. T., Skudlarski, P., Fulbright, R. K., Bronen, R. A., Shankweiler, D. P., Katz, L., Fletcher, J. M., & Gore, J. C. (1996). Cerebral organization of component processes in reading. *Brain, 119*, 1221–1238.

Radeau, M., Besson, M., Fonteneau, E., & Castro, S. L. (1998). Semantic, repetition and rime priming between spoken words: behavioral and electrophysiological evidence. *Biological Psychology, 48*(2), 183–204.

Rauschecker, J. P. (1998). Cortical processing of complex sounds. *Current Opinion in Neurobiology, 8*(4), 516–521.

Rauschecker, J. P., & Scott, S. K. (2009). Maps and streams in the auditory cortex: nonhuman primates illuminate human speech processing. *Nature Neuroscience, 12*(6), 718–724.

Rayman, J., & Zaidel, E. (1991). Rhyming and the right hemisphere. *Brain and Language, 40*(1), 89–105.

Rogalsky, C., & Hickok, G. (2011). The role of Broca's area in sentence comprehension. *Journal of Cognitive Neuroscience, 23*(7), 1664–1680.

Rogalsky, C., Matchin, W., & Hickok, G. (2008). Broca's area, sentence comprehension, and working memory: an fMRI Study. *Frontiers in Human Neuroscience, 2,* 14.

Rosen, S. (1992). Temporal information in speech: acoustic, auditory and linguistic aspects. *Philosophical Transactions: Biological Sciences, 336*(1278), 367–373.

Rossell, S. L., Price, C. J., & Nobre, A. C. (2003). The anatomy and time course of semantic priming investigated by fMRI and ERPs. *Neuropsychologia, 41*(5), 550–564.

Rothermich, K., & Kotz, S. A. (2013). Predictions in speech comprehension: fMRI evidence on the meter-semantic interface. *NeuroImage, 70,* 89–100.

Rugg, M. D. (1984a). Event-related potentials and the phonological processing of words and non-words. *Neuropsychologia, 22*(4), 435–443.

Rugg, M. D. (1984b). Event-related potentials in phonological matching tasks. *Brain and Language, 23*(2), 225–240.

Rugg, M. D., & Barrett, S. E. (1987). Event-related potentials and the interaction between orthographic and phonological information in a rhyme-judgment task. *Brain and Language, 32(*2), 336–361.

Rumsey, J. M., Andreason, P., Zametkin, A. J., Aquino, T., King, A. C., Hamburger, S. D., et al. (1992). Failure to activate the left temporoparietal cortex in dyslexia. An oxygen 15 positron emission tomographic study. *Archives of Neurology, 49*(5), 527–534.

Saberi, K., & Perrott, D. R. (1999). Cognitive restoration of reversed speech. *Nature, 398*(6730), 760.

Scheich, H., Brechmann, A., Brosch, M., Budinger, E., & Ohl, F. W. (2007). The cognitive auditory cortex: task-specificity of stimulus representations. *Hearing Research, 229*(1-2), 213–224.

Schmidt, C. F., Zaehle, T., Meyer, M., Geiser, E., Boesiger, P., & Jancke, L. (2008). Silent and continuous fMRI scanning differentially modulate activation in an auditory language comprehension task. *Human Brain Mapping, 29*(1), 46–56.

Schmidt-Kassow, M., & Kotz, S. A. (2009). Event-related brain potentials suggest a late interaction of meter and syntax in the P600. *Journal of Cognitive Neuroscience, 21*(9), 1693–1708.

Schönwiesner, M., Rübsamen, R., & VonCramon, D. Y. (2005). Hemispheric asymmetry for spectral and temporal processing in the human antero-lateral auditory belt cortex. *The European Journal of Neuroscience, 22*(6), 1521–1528.

Schwartz, J., & Tallal, P. (1980). Rate of acoustic change may underlie hemispheric specialization for speech perception. *Science, 207*(4437), 1380–1381.

Schwarzbauer, C., Davis, M. H., Rodd, J. M., & Johnsrude, I. (2006). Interleaved silent steady state (ISSS) imaging: a new sparse imaging method applied to auditory fMRI. *NeuroImage, 29*(3), 774–782.

Scott, S. K., Blank, C. C., Rosen, S., & Wise, R. J. (2000). Identification of a pathway for intelligible speech in the left temporal lobe. *Brain, 123*, 2400–2406.

Sergent, J., Zuck, E., Lévesque, M., & MacDonald, B. (1992). Positron emission tomography study of letter and object processing: empirical findings and methodological considerations. *Cerebral Cortex, 2*(1), 68–80.

Slevc, L. R., Martin, R. C., Hamilton, A. C., & Joanisse, M. F. (2011). Speech perception, rapid temporal processing, and the left hemisphere: a case study of unilateral pure word deafness. *Neuropsychologia, 49*(2), 216–230.

Smith, E. E., & Jonides, J. (1999). Storage and executive processes in the frontal lobes. *Science, 283*(5408), 1657–1661.

Specht, K. (2014). Neuronal basis of speech comprehension. *Hearing Research, 307*, 121–135.

Spitsyna, G., Warren, J. E., Scott, S. K., Turkheimer, F. E., & Wise, Richard J. S (2006). Converging language streams in the human temporal lobe. *The Journal of Neuroscience, 26*(28), 7328–7336.

Stanovich, K., Cunningham, A., & Cramer, B. (1984). Assessing phonological awareness in kindergarten-children - issues of task comparability. *Journal of Experimental Child Psychology, 38*, 175–190.

Stanovich, K. E., & Cunningham, A. E. (1992). Studying the consequences of literacy within a literate society: the cognitive correlates of print exposure. *Memory & Cognition, 20*(1), 51–68.

Steinbrink, C., Ackermann, H., Lachmann, T., & Riecker, A. (2009). Contribution of the anterior insula to temporal auditory processing deficits in developmental dyslexia. *Human Brain Mapping, 30*(8), 2401–2411.

Sterzer, P., & Kleinschmidt, A. (2010). Anterior insula activations in perceptual paradigms: often observed but barely understood. *Brain Structure & Function, 214*(5-6), 611–622.

Stowe, L., Haverkort, M., & Zwarts, F. (2005). Rethinking the neurological basis of language. *Lingua, 115*, 997–1042.

Studdert-Kennedy, M., & Shankweiler, D. (1970). Hemispheric specialization for speech perception. *The Journal of the Acoustical Society of America, 48*(2), 579–594.

Sweet, L. H., Paskavitz, J. F., Haley, A. P., Gunstad, J. J., Mulligan, R. C., Nyalakanti, P. K., & Cohen, R. A. (2008). Imaging phonological similarity effects on verbal working memory. *Neuropsychologia, 46*(4), 1114–1123.

Tallal, P., Miller, S., & Fitch, R. H. (1993). Neurobiological basis of speech: a case for the preeminence of temporal processing. *Annals of the New York Academy of Sciences, 682*, 27–47.

Tervaniemi, M., & Hugdahl, K. (2003). Lateralization of auditory-cortex functions. *Brain Research Reviews, 43*(3), 231–246.

Tettamanti, M., & Weniger, D. (2006). Broca's area: a supramodal hierarchical processor? *Cortex, 42*(4), 491–494.

Thiel, A., Haupt, W. F., Habedank, B., Winhuisen, L., Herholz, K., Kessler, J., Markowitsch, H. J., & Heiss, W. D. (2005). Neuroimaging-guided rTMS of the left inferior frontal gyrus interferes with repetition priming. *NeuroImage, 25*(3), 815–823.

Thoenissen, D., Zilles, K., & Toni, I. (2002). Differential involvement of parietal and precentral regions in movement preparation and motor intention. *The Journal of Neuroscience, 22*(20), 9024–9034.

Treiman, R., & Kessler, B. (1995). In defense of an onset-rime syllable structure for English. *Language and Speech, 38*, 127–142.

Tun, P. A., Williams, V. A., Small, B. J., & Hafter, E. R. (2012). The effects of aging on auditory processing and cognition. *American Journal of Audiology*, 21(2), 344–350.

Turken, A. U., & Dronkers, N. F. (2011). The neural architecture of the language comprehension network: converging evidence from lesion and connectivity analyses. *Frontiers in Systems Neuroscience*, *5*, 1.

Turner, R. S., Kenyon, L. C., Trojanowski, J. Q., Gonatas, N., & Grossman, M. (1996). Clinical, neuroimaging, and pathologic features of progressive nonfluent aphasia. *Annals of Neurology*, *39*(2), 166–173.

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., Mazoyer, B., & Joliot, M. (2002). Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *NeuroImage*, *15*(1), 273–289.

Vaden, K. I., Muftuler, L. T., & Hickok, G. (2010). Phonological repetition-suppression in bilateral superior temporal sulci. *NeuroImage*, *49*(1), 1018–1023.

van Alphen, P., Bree, E. de, Gerrits, E., Jong, J. de, Wilsenach, C., & Wijnen, F. (2004). Early language development in children with a genetic risk of dyslexia. *Dyslexia*, *10*(4), 265–288.

Van Lancker Sidtis, D Pachana, N., Cummings, J. L., & Sidtis, J. J. (2006). Dysprosodic speech following basal ganglia insult: toward a conceptual framework for the study of the cerebral representation of prosody. *Brain and Language*, *97*(2), 135–153.

Vandenberghe, R., Nobre, A. C., & Price, C. J. (2002). The response of left temporal cortex to sentences. *Journal of Cognitive Neuroscience*, *14*(4), 550–560.

Vigneau, M., Beaucousin, V., Herve, P. Y., Duffau, H., Crivello, F., Houde, O., Mazoyer, B., & Tzourio-Mazoyer, N. (2006). Meta-analyzing left hemisphere language areas: Phonology, semantics, and sentence processing. *NeuroImage*, *30*(4), 1414–1432.

Vigneau, M., Beaucousin, V., Hervé, P.-Y., Jobard, G., Petit, L., Crivello, F., et al. (2011). What is right-hemisphere contribution to phonological, lexico-semantic, and sentence processing? Insights from a meta-analysis. *NeuroImage*, *54*(1), 577–593.

Vloedgraven, J. M., & Verhoeven, L. (2007). Screening of phonological awareness in the early elementary grades: An IRT approach. *Annals of Dyslexia*, *57*, 33–50.

Wagensveld, B., Segers, E., van Alphen, P., Hagoort, P., & Verhoeven, L. (2012). A neurocognitive perspective on rhyme awareness: The N450 rhyme effect. *Brain Research*, *1483*, 63–70.

Wagensveld, B., van Alphen, P., Segers, E., Hagoort, P., & Verhoeven, L. (2013). The neural correlates of rhyme awareness in preliterate and literate children. *Clinical Neurophysiology, 124*(7), 1336–1345.

Warrier, C., Wong, P., Penhune, V., Zatorre, R., Parrish, T., Abrams, D., & Kraus, N. (2009). Relating structure to function: Heschl's gyrus and acoustic processing. *The Journal of Neuroscience, 29*(1), 61–69.

Webb, M.-Y., Schwanenflugel, P. J., & Kim, S. (2004). A Construct Validation Study of Phonological Awareness for Children entering Pre-kindergarten. *Journal of Psychoeducational Assessment,* 22, 304-319

Weiller, C., Bormann, T., Saur, D., Musso, M., & Rijntjes, M. (2011). How the ventral pathway got lost – And what its recovery might mean. *Brain and Language, 118*(1-2), 29–39.

Wernicke, C. (Ed.) (1874). Der aphasische Symptomencomplex: eine psychologische Studie auf anatomischer Basis. Breslau: Max Cohn & Weigert.

Wildgruber, D., Ackermann, H., Klose, U., Kardatzki, B., & Grodd, W. (1996). Functional lateralization of speech production at primary motor cortex: a fMRI study. *Neuroreport, 7*(15-17), 2791–2795.

Wise, R. J., Scott, S. K., Blank, S. C., Mummery, C. J., Murphy, K., & Warburton, E. A. (2001). Separate neural subsystems within 'Wernicke's area'. *Brain, 124*, 83–95.

Wood, C., & Terrell, C. (1998). Pre-school phonological awareness and subsequent literacy development. *Educational Psychology, 18*, 253–274.

Xu, B., Grafman, J., Gaillard, W. D., Ishii, K., Vega-Bermudez, F., Pietrini, P., Reeves-Tyer, P., diCamillo, P., & Theodore, W. (2001). Conjoint and extended neural networks for the computation of speech codes: the neural basis of selective impairment in reading words and pseudowords. *Cerebral Cortex. 11*(3), 267–277.

Yang, Y., Engelien, A., Engelien, W., Xu, S., Stern, E., & Silbersweig, D. A. (2000). A silent event-related functional MRI technique for brain activation studies without interference of scanner acoustic noise. *Magnetic Resonance in Medicine, 43*(2), 185–190.

Zaehle, T., Wüstenberg, T., Meyer, M., & Jäncke, L. (2004). Evidence for rapid auditory perception as the foundation of speech processing: a sparse temporal sampling fMRI study. *The European Journal of Neuroscience, 20*(9), 2447–2456.

Zaehle, T., Geiser, E., Alter, K., Jancke, L., & Meyer, M. (2008). Segmental processing in the human auditory dorsal stream. *Brain Research, 1220*, 179–190.

Zaehle, T., Jancke, L., Herrmann, C., & Meyer, M. (2009). Pre-attentive Spectro-temporal Feature Processing in the Human Auditory System. *Brain Topography, 22*(2), 97–108.

Zaehle, T., Schmidt, C. F., Meyer, M., Baumann, S., Baltes, C., Boesiger, P., & Jancke, L. (2007). Comparison of "silent" clustered and sparse temporal fMRI acquisitions in tonal and speech perception tasks. *NeuroImage, 37*(4), 1195–1204.

Zatorre, R. J., & Belin, P. (2001). Spectral and temporal processing in human auditory cortex. *Cerebral Cortex, 11*(10), 946–953.

Zatorre, R. J., Evans, A. C., & Meyer, E. (1994). Neural mechanisms underlying melodic perception and memory for pitch. *The Journal of Neuroscience, 14*(4), 1908–1919.

Zatorre, R. J., Evans, A. C., Meyer, E., & Gjedde, A. (1992). Lateralization of phonetic and pitch discrimination in speech processing. *Science, 256*(5058), 846–849.

Zatorre, R. J., Meyer, E., Gjedde, A., & Evans, A. C. (1996). PET studies of phonetic processing of speech: review, replication, and reanalysis. *Cerebral Cortex, 6*(1), 21–30.

Zatorre, R. J., Belin, P., & Penhune, V. B. (2002). Structure and function of auditory cortex: music and speech. *Trends in Cognitive Sciences*, 6(1), 37–46.

Zatorre, R. J., & Gandour, J. T. (2008). Neural specializations for speech and pitch: moving beyond the dichotomies. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences, 363*(1493), 1087–1104.

Zekveld, A. A., Heslenfeld, D. J., Festen, J. M., & Schoonhoven, R. (2006). Top-down and bottom-up processes in speech comprehension. *NeuroImage, 32*(4), 1826–1836.

Zhang, L., Shu, H., Zhou, F., Wang, X., & Li, P. (2010). Common and distinct neural substrates for the perception of speech rhythm and intonation. *Human Brain Mapping, 31*(7), 1106–1116.

Zurif, E., & Mendelsohn, M. (1972). Hemispheric specialization for the perception of speech sounds: the influence of intonation and structure. *Attention, Perception, and Psychophysics, 11*(5), 329–332.

Zurowski, B., Gostomzyk, J., Grön, G., Weller, R., Schirrmeister, H., Neumeier, B., Spitzer, M., Reske, S. N., & Walter, H. (2002). Dissociating a common working memory network from different neural substrates of phonological and spatial stimulus processing. *NeuroImage, 15*(1), 45–57.

LIST OF ABBREVIATIONS

AST	Asymmetric sampling in time
BA	Brodmann area
BOLD	Blood oxygen level dependent
EEG	Electroencephalography
ERP	Event-related potentials
FOP	Frontal operculum
fMRI	Functional magnetic resonance imaging
FWE	Familywise error
HG	Heschl's gyrus
HIP	Hippocampus
IFG	Inferior frontal gyrus
IFGop	Inferior frontal gyrus, opercular part
IPL	Intraparietal lobe
ITG	Inferior temporal gyrus
MNR	Metrical non-rhymed
MR	Metrical rhymed
MTG	Middle temporal gyrus
NMNR	Non-metrical non-rhymed
NMR	Non-metrical rhymed
NR	Non-rhymed
pSTG	Posterior superior temporal gyrus
PET	Positron emission tomography
PT	Planum temporale
R	Rhymed
RT	Reaction time
ROI	Region of interest
ROP	Rolandic operculum
SMG	Supramarginal gyrus
STG	Superior temporal gyrus
STS	Superior temporal sulcus
WM	Working memory

CURRICULUM VITAE

PERSONAL DETAILS

Name	Martina Andrea Hurschler
Date of birth	June 8 1981, Lucerne LU

EDUCATION

2009 – 2014	Ph.D. student University of Zurich, Department Neuropsychology
2005 – 2009	Studies of Psychology (MSc), University of Zurich,
	Major Subject: Neuropsychology
	First minor subject: Psychopathology (childhood and adolescence)
	Second minor subject: Social and preventive medicine

PUBLICATIONS

- Hurschler M.A., Liem, F., Oechslin, M., Stämpfli, P., Meyer, M. (2015). fMRI reveals lateralized pattern of brain activity modulated by the metrics of stimuli during auditory rhyme processing. *Brain and Language 147,* 41-50.
- Hurschler M.A., Liem, F., Jäncke, L., Meyer M. (2012). Right and left perisylvian cortex and left inferior frontal cortex mediate sentence-level rhyme detection in spoken language as revealed by sparse fMRI. *Human Brain Mapping 34(12),* 3182-3192.
- Liem F., Hurschler M.A., Jäncke, L., Meyer M. (2014). On the planum temporale lateralization in suprasegmental speech perception: evidence from a study investigating behavior, structure, and function. *Human Brain Mapping 35(4*): 1779-1789.